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# JOURNAL OF THE
# MARINE BIOLOGICAL ASSOCIATION
## OF THE UNITED KINGDOM

*Printed in Great Britain at the University Press, Cambridge*
*(Brooke Crutchley, University Printer)*
*and published by the Cambridge University Press*
*(Cambridge, and Bentley House, London)*

*Agents for Canada and India: Macmillan*

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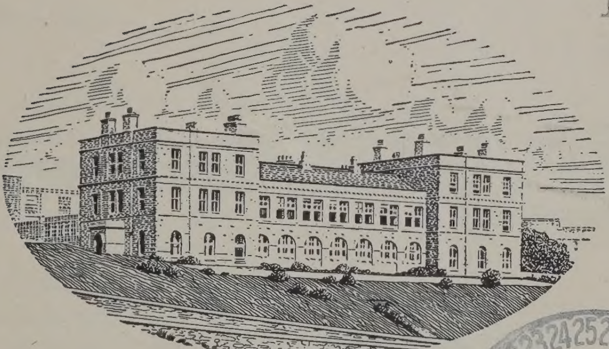

THE PLYMOUTH LABORATORY

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VOLUME XXX

1951–1952

CAMBRIDGE
AT THE UNIVERSITY PRESS
1952

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# ERRATA

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Page 170. Table III. At station 11 there are 4 *Abra alba* and no *A. nitida*.
175. Table VII. At station 28 there are 2 *Abra alba* and no *A. nitida*.

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Page 7. One line from bottom. *For* 7. iv. 50 *read* 7. iv. 49.
20. Explanation of Plate I, figs. 1 and 2. *For* 7. iv. 50 *read* 7. iv. 49.
84. Third paragraph, first line. *For* klino-kinesis *read* klino-taxis.
No. 2, back page of cover. Line 2. For *Sipirorbis* read *Spirorbis*.
Page 138. Para. 4, line 6. *For* isohyaline *read* isohaline.
489. Fig. 13:

Lines of equal oxygen content.

*For* 4·5 ml./l., *read* $4{\cdot}5_8$ ml./l.
,, 5·0 ,, ,, $5{\cdot}0_7$ ,,
,, 5·5 ,, ,, $5{\cdot}5_8$ ,,
,, 6·0 ,, ,, $6{\cdot}0_8$ ,,

Lines of equal percentage saturation with oxygen.

*For* 70 % *read* $71{\cdot}_0$ %
,, 80 % ,, $81{\cdot}_1$ %
,, 90 % ,, $91{\cdot}_3$ %
,, 95 % ,, $96{\cdot}_3$ %

# A BIOLOGICAL DIFFERENCE BETWEEN NATURAL SEA WATERS

By Douglas P. Wilson, D.Sc., F.R.P.S.
Zoologist at the Plymouth Laboratory

(Plates I and II)

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## INTRODUCTION

The work of F. S. Russell on plankton animals as indicators of different water masses, particularly the species *Sagitta setosa* J. Müller and *S. elegans* Verrill, and of Atkins, Harvey and Cooper on plant nutrients, have pointed the conclusion that the water in the English Channel, in the neighbourhood of Plymouth, was consistently richer in nutrients and plankton in the 5 or 6 years prior to about 1930 than it has been at any time since. (See Russell, 1935, 1936*a*, 1939; Cooper, 1938; Armstrong & Harvey, 1950; Harvey, 1950.) The comparative infertility of the sea in this area in the 1930's, and until the present time, has been shown not only by the low winter phosphate maximum, and by the sparse plankton characterized by the presence of *S. setosa*, but also by the reduced numbers of young fishes surviving their early larval stages after the summer spawning (Russell, 1939).

It was during the 1930's that I experienced much frustration in numerous attempts to rear the larvae of various species of polychaetes. It may be that the species concerned would in any event have proved difficult, but the meagre results obtained for energy expended, especially when compared with the easier successes of the later years of the 1920's, gradually led to a suspicion that there might be another explanation. As it became clearer, from the work of Russell and Cooper, that local planktonic and hydrographic conditions had changed, it occurred to me that, quite apart from considerations of nutrients and plankton food, the local sea water which I was using for my work might itself be a less favourable medium for developing eggs and larvae than formerly. It seemed at least possible that some species would develop more readily in *elegans* than in *setosa* water, and perhaps vice versa. Before 1930 the water used for rearing would very likely have been *elegans* water, while after that date *setosa* water was probably employed. All water used for rearing had been passed through Berkefeld filter candles so that plankton organisms in the water had been removed, any necessary food having been provided from artificial cultures, generally of the diatom *Nitzschia*. Thus if *setosa* water was less favourable than *elegans* water for eggs and larvae, it was not due to the contained plankton. It might be that *setosa* water lacked some vital substance, or alternatively contained in minute amount something harmful to certain species. The effect might be directly on the larvae themselves, or it might be on the maturation of the germ cells so that in some species eggs produced and fertilized under *setosa* conditions are less viable than those matured in an *elegans* environment.

This possibility had become apparent even before 1939, and on discussing the matter with Dr Cooper that year I found that he also, but from a different direction, was approaching similar conclusions. We considered the practicability of obtaining *elegans* water from the westward, but before this could be done war broke out and made it impossible, and it was not until fairly recently that the two kinds of water could actually be tested.

The first tests were made in the summer of 1948. I was at that time engaged in experimenting with larvae of the small polychaete *Ophelia bicornis*. Usually there is little difficulty in rearing this species, but that particular summer several cultures had unaccountably failed. The question of the water was again raised, and on his next cruise to the westward Dr Cooper very kindly obtained some *elegans* water for me. Using this water, exceptionally fine rearings were obtained; at the same time some direct comparative tests of this *elegans* water with our ordinary 'Outside' water were also made. The results were so encouraging (Exps. 1 and 2, pp. 3–5) that the following spring, and again the next year, more extensive tests were undertaken, using plutei of *Echinus esculentus* which are specially sensitive to cultural conditions. The larvae of another polychaete, *Sabellaria alveolata*, were also tested.

Before detailing the experiments the names adopted for the waters must be explained. It is thought better to refer to them by their location, for although in these experiments the water from the Celtic sea (definition in Cooper & Vaux, 1949, p. 750) always contained typical *elegans* plankton, and the Outside water consistently contained a very sparse zooplankton (a characteristic of *setosa* water) in a further series this might not be so. The plankton was taken, usually at the same time as the water, with a 2 m. stramin ring-trawl. Outside water derives its name from the fact that it is got off Plymouth, *outside* the breakwater and well out to sea, often from beyond the Eddystone.

For much helpful discussion I wish to thank especially Mr F. S. Russell, Dr H. W. Harvey and Dr L. H. N. Cooper. Dr Cooper and Mr F. A. J. Armstrong have given invaluable help technically; they collected, often under

trying conditions, most of the samples of water tested, and they are responsible for the water analyses and other hydrographical data given in this paper. The plankton was examined by Mr P. G. Corbin who kindly supplied the descriptions.

## THE EXPERIMENTS

### *General Method*

All glassware was cleaned with warm concentrated sulphuric acid and thoroughly washed. Throughout, special attention was given to cleanliness and the avoidance of contamination. Care was taken to treat both sides of an experiment alike. All vessels containing water and larvae undergoing comparative tests were kept side by side under identical lighting and temperature conditions. All waters were filtered through Berkefeld filter candles. In the earlier experiments the test vessels were glass finger bowls of diameter approximately 12·5 cm. and total capacity 500 c.c. They were filled to just over half capacity. In the 1950 experiments, with *Echinus esculentus*, crystallizing dishes 7 cm. in diameter and of approximately 160 c.c. total capacity were used. They were about two-thirds filled, water levels being equal in all dishes in any one experiment.

### *Experiments with* Ophelia bicornis *Sav.*

Fertilizations were made by slitting open mature worms to obtain eggs and sperms. The fertilized eggs were then divided equally into two portions, each of which was thoroughly washed with one of the waters being tested. After 16–20 hr. surface-swimming larvae were poured off into new bowls to separate them from undeveloped eggs, or abnormal larvae which had not swum up. Additional water was added to the new bowls and the levels equalized.

*Experiment* 1

*Celtic sea water* collected from the sea surface by means of a wooden bucket.
Position: 50° 00′ N., 7° 10′ W. Sounding: 110 m.
Date: 30. vi. 48. Time: 04.40 hr. G.M.T.
Ship: R.V. *Sabella*, with Dr L. H. N. Cooper.
Conditions: rough sea and heavy confused swell, in spite of which salinity at 0·5 m. was greater by 0·09‰ than at 5 m.
Physical and chemical observations:

| Depth (m.) | Temp. (° C.) | Salinity (‰) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 0·5 | 13·63 | 35·21 | — | 0·06 | — |
| 5 | 13·59 | 35·12 | 0·36 | 0·04 | 0·32 |
| 50–107 | 9·83 | 35·22 | 0·70 | 0·44–0·51 | 0·23 |
| Integral mean of water column | — | — | 0·58 | 0·33 | 0·25 |

The *Outside water* was from the ordinary laboratory stock, recently collected from the sea surface well offshore from Plymouth. Very little plankton had been present in the area throughout June and early July.

On the way home from the Celtic sea, hydrographical observations were made at station E 1 but no water was collected for the present work.

Position: E 1, 50° 02′ N., 4° 22′ W.

Date: 1. vii. 48.

| Depth (m.) | Temp. (° C.) | Salinity (°/₀₀) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 0·5 | 13·55 | 35·34 | 0·39 | 0·04 | 0·35 |
| 5 | 13·53 | 35·34 | 0·39 | 0·01 | 0·38 |
| 50–70 | 11·50 | 35·37 | 0·53 | 0·31 | 0·22 |
| Integral mean of water column | — | — | 0·52 | 0·23 | 0·29 |

The Channel was more saline by about 0·2°/₀₀, otherwise the two stations differed only in the bottom water which in the Celtic sea was colder and richer in inorganic and consequently in total phosphorus. The phosphorus results do not suggest that *minimum* organic production had been markedly different at the two stations.

The fertilizations of *Ophelia* were made in Celtic water on 8. vii. 48. Three separate fertilizations were made, using three females for each. One male was used to fertilize all the eggs. Each fertilization was immediately divided equally between the two kinds of water and treated as already described.

Results are summarized in Table I. They are positive in favour of Celtic water. After about a week there were many more abnormalities in Outside than in Celtic water. Prototrochal cilia were lost, without proper metamorphosis, earlier in Outside than in Celtic water. In Outside water very many larvae stuck together in large masses; they did so hardly at all in Celtic water. Larvae in Celtic water outlived those in Outside water.

TABLE I. EXP. 1. FERTILIZATIONS OF *OPHELIA BICORNIS* MADE ON 8 JULY 1948

| | Fertilization no. 1 Condition of larvae in | | Fertilization no. 2 Condition of larvae in | | Fertilization no. 3 Condition of larvae in | |
|---|---|---|---|---|---|---|
| | Celtic water | Outside water | Celtic water | Outside water | Celtic water | Outside water |
| 15. vii. 48 | Very good | Good | Very good | Good | Very good | Good |
| 19. vii. 48 | Good | Fairly good | Good | Fairly good | Good | Fairly good |
| 24. vii. 48 | Good | Poor | Very good | Fair | Very good | Fair |
| 28. vii. 48 | Fairly good, majority alive | Poor, majority dead | Good, all living | Poor, many dead | Very good, all living | Poor, many dead |

*Experiment* 2.

Particulars of waters as for Exp. 1.

The fertilizations of *Ophelia* were made in Celtic water on 12. vii. 48. Three separate fertilizations were made, using one female for each. One male was used for all three. Each fertilization was immediately divided into both kinds of water, as already described.

Results are summarized in Table II. They are positive in favour of Celtic water. On 17. vii. 48 large numbers of larvae in all three bowls of Outside water were stuck together in very big masses, but larvae in Celtic water were not so massed together and appeared to be much healthier. On this date considerable numbers of larvae were removed from two bowls of Celtic water (Fertilizations 5 and 6) to supply experiments with which this paper is not concerned. After this date these two bowls therefore contained fewer larvae than the corresponding bowls of Outside water.

TABLE II. EXP. 2. FERTILIZATIONS OF *OPHELIA BICORNIS* MADE ON 12 JULY 1948

| | Fertilization no. 4 Condition of larvae in | | Fertilization no. 5 Condition of larvae in | | Fertilization no. 6 Condition of larvae in | |
|---|---|---|---|---|---|---|
| | Celtic water | Outside water | Celtic water | Outside water | Celtic water | Outside water |
| 17.vii.48 | Very good | Good | Very good | Good | Very good | Good |
| 24.vii.48 | Very good | Fairly good | — | — | — | — |
| 26.vii.48 | — | — | Very good | Good | Good | Very poor, many dead |
| 28.vii.48 | Very good | Fairly good | Good | Fair | Good | Almost all dead |

### *Experiments with* Echinus esculentus *L.*

Recently trawled urchins were used, if possible immediately after trawling, or within a day or two. For each experiment one ripe female and one ripe male were selected by microscopic examination of the gonads after removal of the oral portion of the test. The aboral surfaces were then well rinsed and the inverted urchins spawned into beakers of filtered sea water, either Outside or Celtic. The fertilized eggs were at once divided equally between two beakers and thoroughly washed with six to eight changes, one of Outside water and the other of Celtic water. From each, after thorough stirring to distribute the eggs evenly, equal volumes were removed in a glass dipper to vessels already containing equal volumes of the waters to be tested. Thus very nearly the same number of eggs was added to all vessels. Three or more vessels of each kind of water were tested in a single experiment. After 24 hr. swimming blastulae were poured off into a second set of vessels, to separate them from undeveloped or abnormally developing eggs on the bottom, except in the 1950 experiments when this was not necessary. The water-levels in the second set of vessels were equalized.

### *Experiment* 3

*Celtic sea water* collected from the sea surface by means of a wooden bucket.

Position: 50° 36′ N., 8° 04′ W. (over Labadie Bank). Sounding: 70 m.

Date: 10. iii. 49. Time: 01.15 hr.

Ship: R.V. *Sabella* with Dr L. H. N. Cooper.

Conditions: heavy swell immediately following moderate gale (Beaufort Force 7). Vertical mixing should have been considerable.

Plankton: night haul rich with abundant *Sagitta elegans*, large *Aglantha*, Euphausians, etc. No sign of phytoplankton.

Physical and chemical observations were:

| Depth (m.) | Temp. (° C.) | Salinity (°/₀₀) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 5 | 9·95 | 35·24 | 0·69 | 0·51 | 0·18 |
| 25 | 9·98 | 35·23 | 0·76 | 0·50 | 0·26 |
| 60 | 9·98 | 35·23 | 0·79 | 0·49 | 0·30 |
| Integral mean of water column | — | — | 0·76 | 0·50 | 0·26 |

*Outside sea water* collected from the sea surface by means of a wooden bucket by M.F.V. *Sula* during third week of March 1949; exact position unknown. Ordinary laboratory routine collection in glass carboys which had contained sulphuric acid and had previously been well washed out.

Plankton (routine daylight haul 2 miles east of Eddystone) on 21. iii. 49, very, very sparse, hardly any zooplankton, one *Sagitta setosa* present. No sign of phytoplankton.

Physical and chemical observations at station E 1 were:

| Depth (m.) | Temp. (° C.) | | Salinity (°/₀₀) | | Phosphorus (mg.-atom/m.$^3$) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Total | | Inorganic | | Organic | |
| | 1. iii. 49 | 13. iv. 49 | 1. iii. 49 | 13. iv. 49 | 1. iii. 49 | 13. iv. 49 | 1. iii. 49 | 13. iv. 49 | 1. iii. 49 | 13. iv. 49 |
| Surface | 10·1 | — | 35·38 | — | 0·7 | — | 0·43 | — | 0·08 | — |
| 0·5 | — | 9·90 | — | 35·37 | — | 0·53 | — | 0·28 | — | 0·25 |
| 5 | 10·06 | 9·88 | 35·35 | 35·38 | 0·41 | 0·47 | 0·38 | 0·31 | 0·03 | 0·16 |
| 50–70 | 10·02 | 9·86 | 35·35 | 35·30 | 0·44 | 0·45 | 0·41 | 0·32 | 0·04 | 0·13 |
| Integral mean of water column | 10·03 | 9·87 | 35·35 | 35·29 | 0·44 | 0·47 | 0·39 | 0·31 | 0·05 | 0·16 |

The Celtic water had evidently been much richer in total phosphorus and by 10. iii there had been more conversion to organic phosphorus than had taken place a month later in the Channel. Again the Channel water was more saline.

An *Echinus esculentus* fertilization was made in Celtic water on 24. iii. 49. Three bowls of each kind of water were tested.

Results are summarized in Table III. They are positive in favour of Celtic water, although the larvae in this water were the first to show shrinkage of flesh on the arms, the skeletal rods protruding uncovered (29. iii. 49). Regeneration of the arms of many larvae took place after 31. iii. 49. There was no regeneration in Outside water, although the bowls were kept until 20. iv. 49.

*Experiment* 4.

Particulars of waters, etc., as for Exp. 3, but another pair of *E. esculentus* used for the fertilization, which was made in Outside water. Three finger bowls of each kind of water were tested.

Results are summarized in Table IV. They are positive in favour of Celtic water, but this fertilization did not do as well as that of Exp. 3. On 28. iii. 49 the larvae in all three bowls of Celtic water were clearly healthier than those in Outside water.

*Experiment* 5.

Particulars of waters, etc., as for Exp. 3.

*E. esculentus* fertilization made in Celtic water on 30. iii. 49. Four bowls of each kind of water were tested and, in addition, there were four bowls of a mixture of approximately equal volumes of both waters. Two bowls of each series were given food (*Nitzschia* and an autotrophic flagellate).

Results are summarized in Table V. They are positive in favour of Celtic water. The Mixed water was almost as good as the Celtic. Feeding made no appreciable difference and did not help the larvae in Outside water. On 6. iv. 49 the pH was the same for all bowls; it did not differ from normal sea water. There was some regeneration of arms of plutei in Outside water after 9. iv. 49, but in only one bowl did this progress to any extent. In this one bowl there were fair numbers of good plutei on 20. iv. 49 when the experiment was ended. Conditions at this time varied from bowl to bowl, rather irrespective of the kind of water.

TABLE III. EXP. 3. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 24 MARCH 1949

| | Condition of larvae in Celtic water (bowls 1–3) | Condition of larvae in Outside water (bowls 4–6) |
|---|---|---|
| 26. iii. 49 | Many at surface, few on bottom | Few at surface, many on bottom |
| 28. iii. 49 | Most at surface, some in mid-water, few on bottom | Some at surface and in mid-water but most on bottom, some dying |
| 29. iii. 49 | Bowl 1: about one-third at surface, a few in mid-water, most on bottom. Bowls 2 and 3: most at surface, few in mid-water, about one-third on bottom. Few dead in all three bowls. In most of the living the flesh of the arms shrinking away | Bowl 4: about one-half mid-water to surface, remainder on bottom. Bowls 5 and 6: fair number between bottom and surface, most on bottom. Many dead in all three bowls. In the living the arms are generally normal. A little shrinkage of flesh |
| 30. iii. 49 | Few at surface, most on bottom | Few at surface, most on bottom |
| 31. iii. 49 | All on or near bottom, unhealthy with shortened arms, some dead | All on or near bottom, unhealthy with shortened arms, many dead |
| 4. iv. 49 | Many at surface or in mid-water, most at bottom, generally short-armed but some long-armed. Some dead | All on bottom, majority dead. Living abnormal, with very short arms or none at all |
| 6. iv. 49 | Numbers at surface or in mid-water, many on bottom, some dead. Swimming larvae with long slender arms, on bottom many with short arms, or with none | All on bottom, a few with short arms, most with none, bodies generally shrunken and abnormal. Majority dead |

TABLE IV. EXP. 4. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 24 MARCH 1949

| | Condition of larvae in Celtic water (bowls 1–3) | Condition of larvae in Outside water (bowls 4–6) |
|---|---|---|
| 26. iii. 49 | Most at surface, few on bottom | Some at surface, most on bottom |
| 28. iii. 49 | Most at surface, some in mid-water, few or none on bottom. A few larvae abnormal | Many at surface and in mid-water, a considerable number on bottom. Many abnormal |
| 29. iii. 49 | Many at surface, few in mid-water, most on bottom. Flesh of arms shrinking from skeletal rods | Some at surface, some in mid-water, most on bottom. Flesh of arms shrinking from skeletal rods |
| 30. iii. 49 | All in poor condition | All in poor condition |

Larvae from Celtic and Outside water were photographed on 7. iv. 50 (Pl. I, figs. 1, 2).

### TABLE V. EXP. 5. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 30 MARCH 1949

| | Condition of larvae in Celtic water (bowls 1–4) | Condition of larvae in Mixed water (bowls 5–8) | Condition of larvae in Outside water (bowls 9–12) |
|---|---|---|---|
| 2. iv. 49 | Many near surface, few near bottom | Many near surface, few near bottom | Many near surface, few near bottom |
| 3. iv. 49 | Many swimming, marked concentration near surface. Many on bottom | Many swimming, some concentration near surface. Many on bottom | Many swimming, some concentration near surface. Many on bottom |
| 5. iv. 49 | Many swimming, some concentration near surface. On bottom some abnormal | Many swimming, some concentration near surface. On bottom some abnormal | Few swimming, most on bottom becoming abnormal |
| 6. iv. 49 | Many normal plutei concentrating near surface. On bottom most becoming abnormal. None dead | Many normal plutei concentrating near surface. On bottom most becoming abnormal. None dead | Very few swimming and all abnormal, those on bottom often very shrunken; some dead |
| 9. iv. 49 | Many normal plutei swimming. Most on bottom abnormal | Many normal plutei swimming. Most on bottom abnormal | Very few swimming and all abnormal. Most on bottom very abnormal or dead |
| 11. iv. 49 | Many normal plutei swimming. Most on bottom abnormal | Many normal plutei swimming. Most on bottom abnormal | Fair number swimming, regenerating arms. Most on bottom very abnormal |

### TABLE VI. EXP. 6. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 21 APRIL 1949

| | Condition of larvae in Celtic water | | Condition of larvae in Outside water | |
|---|---|---|---|---|
| | Bowls 1–3, many larvae per bowl | Bowls 4–6, few larvae per bowl | Bowls 7–9, many larvae per bowl | Bowls 10–12, few larvae per bowl |
| 25. iv. 49 | Many on bottom | — | Few on bottom | — |
| 27. iv. 49 | Very few swimming, most on bottom. All abnormal, many dead | Some normal plutei swimming. On bottom some abnormal, many dead | Few swimming, most on bottom. All abnormal, many dead | Some normal plutei swimming, more than in Celtic water. On bottom some dead, some abnormal, fewer than in Celtic water |
| 3. v. 49 | All dead | Some normal plutei swimming. Some abnormal and some dead on bottom | Bowl 7, all dead. Bowl 8, most dead, a few very abnormal living. Bowl 9, a few swimming, abnormal. Most on bottom, very abnormal, half of them dead | A few normal and more abnormal plutei swimming. A few dead |

*Experiment* 6.

Particulars of Celtic water as for Exp. 3.

*Outside water* collected (from sea surface with wooden bucket) by Mr F. A. J. Armstrong in M.F.V. *Sula*, 13. iv. 49.

Position: E1.

Plankton: daylight haul; very, very sparse, hardly any zooplankton except pilchard eggs in some numbers, one *Sagitta setosa* present. No sign of phytoplankton.

For physical and chemical properties see under Exp. 3.

After the previous experiments the Berkefeld filter candles had been cleaned and re-sterilized. That previously used for filtering Celtic water was here used for Outside water, and vice versa.

*Echinus esculentus* fertilization made in Celtic water on 21. iv. 49. Four bowls of each kind of water were tested; in two bowls larvae were numerous, in two few in number.

Results are summarized in Table VI. They are negative. The fresh Outside water was slightly better than the 6-week-old Celtic water, but neither was good. Larvae did better when there were relatively few per bowl.

*Experiment 7*

*Celtic sea water* collected from 20 m. by means of the pump.

Position: 49° 44′ N., 8° 50′ W. Sounding: 89 m.

Date: 3. v. 49. Time: 20.50 hr. G.M.T.

Ship: R.V. *Sabella* with Dr L. H. N. Cooper.

Conditions: moderate sea, wind force 5.

Plankton: night haul rich with numerous small *Aglantha*, *Tomopteris* and young fish; very abundant plutei, one *Sagitta serratodentata*; *Phaeocystis* abundant. No *Sagitta elegans*.

Physical and chemical observations:

| Depth (m.) | Temp. (° C.) | Salinity (‰) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 0 | 11·48 | 35·37 | 0·37 | 0·10 | 0·27 |
| 5 | 11·50 | 35·35 | 0·33 | 0·17 | 0·16 |
| 20 | 11·50 | 35·36 | 0·34 | 0·12 | 0·22 |
| 40 | 11·18 | 35·37 | 0·45 | 0·15 | 0·30 |
| 80 | 10·82 | 35·38 | 0·63 | 0·40 | 0·23 |
| Integral mean of water column | — | — | 0·46 | 0·23 | 0·23 |

*Outside sea water* collected from sea surface with wooden bucket.

Position: L5, 50° 11′ N., 4° 18′ W. Sounding: 68 m.

Date: 2. v. 49. Time: 10.20 hr. G.M.T.

Ship: M.F.V. *Sula* with Mr F. A. J. Armstrong.

Conditions: fresh north-west wind, sea moderate but increasing.

Plankton: daylight haul, very, very sparse except for pilchard eggs which were abundant. Four *Sagitta setosa*. No sign of phytoplankton.

Physical and chemical observations:

| Depth (m.) | Temp. (° C.) | Salinity (‰) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 5 | 10·23 | 35·26 | 0·37 | 0·15 | 0·22 |
| 10 | 10·17 | 35·27 | 0·38 | 0·15 | 0·23 |
| 25 | 10·08 | 35·28 | 0·42 | 0·22 | 0·20 |
| 50 | 10·08 | 35·31 | 0·51 | 0·26 | 0·25 |
| Integral mean of water column | — | — | 0·43 | 0·21 | 0·22 |

The Channel water was less saline but there was nothing to choose between the waters in terms of phosphorus content.

Berkefeld filter candles again cleaned and changed over.

*Echinus esculentus* fertilization made on 6. v. 49. Six bowls of each kind of water were tested; in three bowls larvae were numerous, in three, few in number.

Results are summarized in Table VII. They are negative; there was no observable difference between comparable bowls of larvae and in neither water was a satisfactory rearing obtained. Bowls with few larvae did a little better than bowls with many. Regeneration of the arms of some plutei took place in both waters after 14. v. 49.

TABLE VII. EXP. 7. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 6 MAY 1949

| | Condition of larvae in Celtic water | | Condition of larvae in Outside water | |
|---|---|---|---|---|
| | Bowls 1–3, many larvae | Bowls 4–6, few larvae | Bowls 7–9, many larvae | Bowls 10–12, few larvae |
| 9. v. 49 | Normal plutei swimming well | Normal plutei swimming well | Normal plutei swimming well | Normal plutei swimming well |
| 11. v. 49 | Very few swimming, most on bottom, becoming abnormal | Some swimming, most on bottom. A few becoming abnormal | Few swimming, most on bottom, becoming abnormal | Some swimming, most on bottom. A few becoming abnormal |
| 14. v. 49 | All on bottom, very abnormal, about half dead | Few swimming, most on bottom, all abnormal | All on bottom, very abnormal, majority dead | Few swimming, most on bottom, all abnormal |
| 16. v. 49 | Mainly dead or dying | Some normal plutei swimming. On bottom some abnormal, some dead | Mainly dead or dying | Some normal plutei swimming. On bottom some abnormal, a few dead |

*Experiment* 8A

*Celtic sea water* collected from 20 m. by means of the pump.

Position: station 64, 50° 33′ N., 8° 51′ W., 25 miles west of Labadie Bank. Sounding: 125 m.

Date: 29. iv. 50. Time: 01.30 hr. G.M.T.

Ship: R.V. *Sabella* with Mr P. G. Corbin.

Conditions: wind force 4, sea slight.

Plankton: night haul, rich, abundant *Sagitta elegans*, two or three *S. serratodentata*, a few *Limacina*, *Tomopteris*, fairly numerous Euphausians. No sign of phytoplankton.

Physical and chemical conditions:

| Depth (m.) | Temp. (° C.) | Salinity (°/₀₀) | Phosphorus (mg.-atom/m.$^3$) | | | Silicate | Plant pigments units under 1 m.$^2$ |
|---|---|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic | | |
| 20 | 9·78 | 35·19 | 0·61 | 0·47 | 0·14 | 3·3 | — |
| Integral mean of water column | — | — | 0·65 | 0·49 | 0·16 | 3·3 | 0 |

*Outside sea water* collected from sea surface with wooden bucket.

Position: E1, 50° 02′ N., 4° 22′ W. Sounding: 74 m.

Date: 3. v. 50. Time: 12.30 hr. G.M.T.

Ship: M.F.V. *Sula* with Dr L. H. N. Cooper.

Plankton: daylight haul, very sparse zooplankton except for abundant pilchard eggs. *Phaeocystis* very abundant.

Physical and chemical conditions:

| Depth (m.) | Temp. (° C.) | Salinity (°/₀₀) | Phosphorus (mg.-atom/m.$^3$) | | |
|---|---|---|---|---|---|
| | | | Total | Inorganic | Organic |
| 0 | 10·86 | 35·14 | 0·49 | 0·13 | 0·33 |
| Integral mean of water column | — | — | 0·52 | 0·17 | 0·35 |

The resources of total phosphorus were greater at the Celtic sea station but *minimum* production as assessed from organic phosphorus was less.

Two new, previously unused Berkefeld filter candles (both of same batch from maker), specially cleaned and sterilized by Mr F. A. J. Armstrong, were used for filtration.

TABLE VIII A. EXP. 8 A. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 5 MAY 1950. THICK CULTURES

| | Condition of larvae in Celtic water (dishes 1–5) | Condition of larvae in mixed water (dishes 6–10) | Condition of larvae in Outside water (dishes 11–15) |
|---|---|---|---|
| 6. v. 50 | Majority concentrating near surface | Majority concentrating near surface | Majority concentrating near surface |
| 8. v. 50 | Most at surface, many in mid-water, few on bottom. Larvae normal | Many at surface, many in mid-water, some on bottom | Some at surface, some in mid-water, most on bottom. Larvae mainly abnormal |
| 9. v. 50 | All swimming with concentration at surface. Normal plutei, abnormalities rare | Many swimming with slight concentration at surface. Fair number on bottom. Larvae mainly normal | Fair number swimming in mid-water, most on bottom. Majority abnormal |
| 10. v. 50 | About 20% swimming. Larvae becoming abnormal, very few dead | About 20% swimming. Larvae fairly normal; fair number dead | Few swimming. Majority abnormal, many dead |
| 12. v. 50 | *Single dish.* Some swimming. Larvae rather abnormal, many dead | *Single dish.* A few living, abnormal. Most dead | *Single dish.* All dead |

*Echinus esculentus* fertilization made in Outside water on 5. v. 50. Three sets, each of five crystallizing dishes, used to test each kind of water and a mixture of both waters in equal proportion. Larvae were highly concentrated, there being several hundreds per dish.

Results are summarized in Table VIII A. They are positive in favour of Celtic water and the mixed water was nearly as good as the Celtic. After 10. v. 50 only one dish of each kind of water was retained.

Two dishes, one of Celtic and the other of Outside water, were photographed side by side on 9. v. 50 (Pl. II, fig. 1). These dishes were typical of all the others. Larvae from both natural waters were photographed on 8. v. 50 (Pl. I, figs. 3, 4).

*Experiment* 8B.

Particulars of waters and fertilization as for Exp. 8A. No mixed water used. Three dishes of each kind of water were on 6. v. 50 supplied with a few surface-swimming blastulae pipetted from the two beakers containing the original fertilization (see p. 5, describing method). On 12. v. 50 to one dish of each kind of water were added, for food, a few drops of a mixture of autotrophic flagellates from culture. This was repeated on 17. v. 50.

Results are summarized in Table VIIIB. They are positive in favour of Celtic water. Larvae did badly in Outside water in spite of the low concentration. Fed larvae did a little better than unfed. Food did little to improve the condition of the larvae in Outside water. The food was eaten, but it may not have been entirely suitable.

TABLE VIIIB. EXP. 8B. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 5 MAY 1950. THIN CULTURES

| | Condition of larvae in Celtic water (dishes 16–18) | | Condition of larvae in Outside water (dishes 19–21) | |
|---|---|---|---|---|
| 6. v. 50 | Most swimming near surface | | Most swimming near surface | |
| 8. v. 50 | All in mid-water or at surface. Larvae normal | | Few at surface, most on bottom. Larvae mainly abnormal | |
| 9. v. 50 | All swimming well up. Normal plutei | | Few swimming, most on bottom. Majority abnormal | |
| 10. v. 50 | All swimming well up. Most plutei well developed | | Some swimming, most on bottom. Majority abnormal | |
| | Dishes 16–17 | Dish 18—fed | Dishes 19–20 | Dish 21—fed |
| 12. v. 50 | Most swimming well, normal. A few slightly abnormal | All normal swimming strongly | All on bottom, all abnormal | All on bottom, majority abnormal |
| 17. v. 50 | Thin-armed plutei swimming well | Normal plutei swimming strongly | All on bottom, all abnormal | One or two swimming. All abnormal |
| 20. v. 50 | Thin-armed plutei swimming well | Normal plutei, half of them swimming. A few dead | All on bottom, abnormal degenerating. A few dead | One or two swimming, one fairly normal pluteus. Majority abnormal degenerating. A few more dead |
| 25. v. 50 | No change | Majority swimming, fairly normal plutei | All on bottom, all abnormal | One or two swimming. All abnormal, often degenerating |

*Experiment* 9.

Particulars of waters as for Exp. 8A, but another portion in another pair of carboys used. The Berkefeld filter candles were cleaned and changed over, that used to filter Celtic water in Exps. 8A and B now being used to filter Outside water, and vice versa.

*E. esculentus* fertilization made in Outside water on 10. v. 50 and, as usual, immediately divided into halves and each washed off with one of the waters.

After $\frac{3}{4}$ hr. it was noticed that most of the still undivided eggs were irregular, not normally rounded, inside the fertilization membrane, and this condition was more marked in Outside than in Celtic water. Two dishes of each kind of water were tested.

Results are summarized in Table IX. They are positive in favour of Celtic water. The difference was shown unusually early; this may have been due to over-ripeness of the eggs, almost all *Echinus* having spawned by this date, those few which had not usually showing histolysis of the ova. The female used for the experiment had only four ovaries. Another factor to be considered is the air temperature which was considerably higher than at any other time during the course of these *Echinus* experiments (both years). The temperature was high from 10. v to 14. v (16–19° C. outside in the shade at 10 a.m., room temperatures were two or three degrees higher) and then dropped several degrees centigrade, remaining relatively cool until the end of the month.

TABLE IX. EXP. 9. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 10 MAY 1950

| | Condition of larvae in Celtic water (dishes 1–2) | Condition of larvae in Outside water (dishes 3–4) |
|---|---|---|
| 11. v. 50 | Blastulae swimming strongly, many at surface | Most on bottom, few swimming |
| 12. v. 50 | Many at surface, few on bottom. Few abnormal, few dead | Few at surface, many on bottom. Abnormals and dead fairly numerous |
| 14. v. 50 | Few swimming; most on bottom abnormal; a few dead | Few swimming, most on bottom, abnormal, about 50% dead |
| 16. v. 50 | Large number swimming but majority on bottom. Arms being regenerated | Almost all dead. A very few living, abnormal |
| 18. v. 50 | Large number swimming strongly, majority on bottom. Further regenerated, some almost normal. A few degenerate, a few dead | All dead |

One dish of each kind of water was photographed side by side on 16. v. 50 (Pl. II, fig. 2). Each dish was typical of all others in its series.

*Experiment* 10.

Particulars of waters as for Exp. 9. This experiment ran concurrently with the latter, a different pair of adults being used for the fertilization, which was made in Celtic water. The female appeared to be partially spawned. The fertilized eggs produced normal fertilization membranes, and cleavage was also normal. Five dishes of each kind of water were tested.

Results are summarized in Table X. They are positive in favour of Celtic water. At first, larvae were weaker than usual in both waters, due possibly to the high air temperatures 10. v–14. v, or to over-ripe ova, or to both. Improvement in the Celtic water coincided with lower air temperatures from 15. v onwards.

TABLE X. EXP. 10. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 10 MAY 1950

| | Condition of larvae in Celtic water (dishes 5–9) | Condition of larvae in Outside water (dishes 10–14) |
|---|---|---|
| 11. v. 50 | Blastulae swimming up to surface | Blastulae swimming up to surface |
| 12. v. 50 | A few swimming up: majority on bottom, some abnormal | A few swimming up: majority on bottom, some abnormal |
| 14. v. 50 | Most on bottom, a few dead | Most on bottom, many dead |
| 15. v. 50 | Some fairly normal plutei swimming well up. Most on bottom, short-armed or armless | None swimming, a large proportion dead. Living larvae very abnormal |
| 17. v. 50 | Many fairly normal plutei swimming, with some concentration at surface. Most on bottom, slightly abnormal | A very few swimming; majority on bottom. All still living very abnormal |

### *Experiment with* Sabellaria alveolata (*L.*)

The success of the early experiments with *Ophelia* and with *Echinus* made it desirable that a trial should be made of other species. So far only one other has been tried; this was *Sabellaria alveolata* which on 12. iv. 49 was collected at Duckpool, near Bude, on the north coast of Cornwall, where it is abundant.

*Experiment* 11.

Particulars of waters as for Exps. 3–5.

A fertilization was made in Celtic water on 13. iv. 49. This was equally divided and washed off in both kinds of water in the usual way. Surface-swimming larvae were decanted into clean bowls on 14. iv. 49. One finger bowl of each kind of water was tested. For food, a few drops of a culture of an autotrophic flagellate was added to both bowls on 14. iv. 49 and again on 20. iv. 49.

TABLE XI. EXP. 11. FERTILIZATION OF *SABELLARIA ALVEOLATA* MADE ON 13 APRIL 1949

| | Condition of larvae in Celtic water | Condition of larvae in Outside water |
|---|---|---|
| 20. iv. 49 | Very few abnormal larvae | Some larvae abnormal, losing bristles |
| 25. iv. 49 | Majority normal, fast swimming. Very few abnormal | Many abnormal. All larvae swimming slowly |
| 27. iv. 49 | Majority normal, fast swimming. Very few abnormal | Many abnormal. All larvae swimming slowly |
| 3. v. 49 | Many abnormal, many dead | Many abnormal, many dead |
| 10. v. 49 | Many abnormal, many dead, but some normal, though lethargic, larvae | Similar to Celtic water |

Results are summarized in Table XI. They are positive in favour of Celtic water. At first larvae in both bowls were similar, but after a week some of these in Outside water were losing the long provisional bristles characteristic of this species (Wilson, 1929). On 25. iv. 49 a big proportion of these larvae were abnormal. They had few or no bristles, shrunken bodies, and were slow swimming. In Celtic water, on this date, there were very few abnormal larvae to be seen; almost all of them were quite normal and fast-swimming. After another week, however, both lots of larvae were in poor condition. They were too crowded for there to have been any possibility of normal growth through their long pelagic development.

### *Other Experiments*

A few other experiments were undertaken; they may be mentioned briefly.

An experiment with *Ophelia bicornis* similar to those already described was begun 5 days later than Exp. 2, using waters from the same collections. This fertilization of *Ophelia* made on 17. vii. 48 gave only a relatively small number of larvae. Those in Celtic water did better than those in Outside water, but the difference was not as great as in the earlier experiment, and in neither water did the larvae do well. The fertilization may have been poor initially, or the Celtic water with longer storage was losing its health-imparting property.

Using the Outside water obtained at L5 on 2. v. 49 (details as for Exp. 7), some tests were made to see if it could be improved by the addition of various substances. A fertilization of *Echinus esculentus* was made in this water on 20. v. 49 and distributed in equal quantity among a number of finger bowls. Addition of soil extract in the proportion used by Gross (1937) to two of the bowls did not improve matters, and the larvae after 5 days were in poorer condition than in three bowls of untreated water. At the suggestion of Dr H. W. Harvey other bowls were treated with vitamin $B_1$ (aneurin hydrochloride), and another set with biotin in various minute proportions. These appeared to have no effect. In this experiment the larvae did rather better than in the same Outside water in Exp. 7, but there was no test of Celtic water with this particular fertilization.

The observation that larvae sometimes regenerated the larval arms led to an experiment to establish the fact more firmly. On 6. iv. 49 a small number of larvae with very short stumpy arms were picked out from one bowl of Celtic water and one of Outside water (bowls forming part of Exp. 5) and placed in new bowls of Celtic water and given autotrophic flagellates for food. On 11. iv. 49 it was observed that a good proportion of these larvae had fairly long arms, and by 20. iv. 49 most of them had normal arms. At first the arms were thin and needle-like, but later were of normal thickness. The larvae transferred from Celtic water did rather better than those from Outside water where a higher proportion failed to regenerate any of the arms.

## DISCUSSION

In experiments of the character just described, one of the most fruitful sources of error would be concealed contamination. In spite of every effort to achieve complete cleanliness, and to treat both sides of an experiment alike, a small unobserved detail of procedure might bias one side more favourably than the other. The technique adopted has been carefully considered with this in mind.

If we take the 1950 experiments alone, it could be pointed out that whereas the Celtic water was collected from 20 m. with a pump, the Outside water was obtained by another ship from the surface with a bucket. The original intention had been to collect both samples with the pump, but weather and other uncontrollable factors had made this impossible. Incidentally, when collecting with the pump the water was sucked through a hose and through the carboy to the pump so that water in the carboy had no contact with the pump itself. A thorough wash through was given before any water was actually taken. Similarly with the wooden bucket method of collection, great care was taken to wash out well the bucket and carboy before the latter was filled. The carboys were thoroughly cleaned in the chemical laboratory ashore, before being taken to sea. (For full details of the method of collecting water samples see Cooper, 1951.) Even so, the objection may be raised that the methods of collection for the 1950 experiments were not the same for both waters. Criticism along these lines, however, can probably be discounted when it is remembered that for the 1949 experiments both waters were collected with wooden buckets.

Another criticism, raised during the experiments, was the possibility of some form of contamination by the Berkefeld filter candles. It might be that one candle affected the water differently from the other. This criticism was met by changing over the filter candles so that the one previously used for Outside water was now used for Celtic water, and vice versa. This was done both in 1949 (see notes to Exps. 6 and 7) and in 1950 (see note to Exp. 9) and in both years, particularly in 1950, it is very evident that the results were unaffected by this procedure (Pl. II, figs. 1, 2). Moreover, the pair of candles used in 1950 was not the same as the pair used in 1949. There is no reason to continue to suspect the filter candles, although it will still be wise to change them over with each new experiment.

The technique used would result in a slight variation in the volume of water and number of larvae per test vessel in each experiment. The variation would, however, be very small and would not be biased in favour of either kind of water. Larvae behaved alike in all test vessels of water of one origin. The small variation in volume and number has therefore no significance. Moreover, consideration of Exp. 7, and comparison of Exp. 8A with 8B, shows that acceleration of the onset of abnormality and death is not unduly accelerated by crowding.

Apart from the experimental details just discussed and discounted no other possible sources of error have been discovered. Thus we conclude that the difference between the waters is real and natural. It should now be considered whether the difference is in any way related to seasonal changes in the plankton, for it is possible that past floras and faunas will have extracted or excreted substances, the absence or presence of which will affect developing larvae. Lucas (1949) has discussed the ecological significance of metabolites, some of them stimulating, others the reverse, in marine and other environments.

The sample of Celtic water which in Exp. 7 proved to be no better than Outside water was observed, before filtration, to contain abundant *Phaeocystis*.

This colonial flagellate was also abundant, before filtration, in the Outside water used in Exps. 8A, 8B and 9. It was not, however, seen in other Outside water samples. It is just possible that it was responsible for the poor condition of the Celtic water used in Exp. 7, but in view of the fact that Outside water, whether it contained *Phaeocystis* or not, was always poor, such an interpretation must be regarded with suspicion. However, the possibility cannot be ruled out entirely.

Except for *Phaeocystis* there is no other correlation of poor water conditions with the observed plankton content, with the possible exception of the occasional abundance of pilchard eggs. It seems therefore more likely that the observed difference is due to something more fundamental, the presence or absence of traces of one or more elements or perhaps traces of organic materials. The results obtained by mixing equal quantities of the two waters (Exps. 5 and 8A) suggest that Celtic water contains something essential for normal development of some species which is lacking in Outside water. Other explanations of the effect of mixing may be possible, but this is perhaps the most reasonable assumption to take as a starting-point for investigation. The importance of various micro-constituents of sea water, especially organic substances and manganese, in the growth of phytoplankton has been emphasized in the work of Harvey (1947, 1949, 1950); it is very probable that the health of zooplankton is likewise dependent on the presence of trace substances, though not necessarily the same substances, and that different species have different requirements.

The bodily forms of the unhealthy plutei (Pl. I, fig. 2) which developed in Outside water are certainly suggestive of a deficiency disease. They show analogous resemblances to plutei experimentally produced by workers concerned with the mechanics of sea-urchin development. With increasing age these abnormal larvae became more and more shrunken, unless they died first.

In the experiments there is evidence (see Exp. 6 and p. 15) that Celtic water deteriorates with storage in ordinary glass carboys at room temperature. Adsorption of the health-promoting factor by the glass is one of various possibilities.

Altogether, during two breeding seasons, eight distinct fertilizations of *Echinus* have been used to test comparatively Celtic water collected on three cruises, and Outside water collected on four separate occasions. In addition, there were separate collections of water for the tests with *Ophelia*; the *Sabellaria* tests used water collected for *Echinus*. Of the eight *Echinus* tests, six were positive in favour of the Celtic water and two were neutral. Possible reasons for the two latter have already been discussed above. The *Ophelia* and *Sabellaria* tests were all positive in favour of Celtic water. In all these experiments the only good rearings have been in Celtic water and all Outside water rearings have been bad. It does not follow, however, that Outside water is always bad. At present, the most that can be inferred is that good rearings are more likely to be obtained by using Celtic water than by using water from the Channel in the region of the Eddystone. So far, no comparative tests have been made with inshore water.

This is the first observation that has been made to show that the difference in bottom faunas from one region to another may be related to the ability, or otherwise, of larval stages to develop in the overlying water mass. For instance, *Luidia ciliaris* (Philippi) is at the present time infrequent off Plymouth where about eighteen years ago it was common, but it is known that its larvae are indicators of *elegans* water and were present in the area when it was covered with *elegans* water (Russell, 1936 *b*, p. 597). Other species dependent to a greater or lesser extent on *elegans* water are likely to have been adversely affected when that water mass moved away from the area. Thus *Munida bamffica* (Pennant), formerly abundant on the Plymouth trawling grounds, is now at best exceedingly rare, while there has been a reduction in the abundance of *Echinus esculentus* itself which when needed in quantity has to be trawled more to the westward than formerly. *Sabellaria alveolata*, although still present at the mouth of the Erme estuary, also seems less common than it used to be. It must not be thought, however, that the fauna of the Plymouth area shows a general all-round reduction; on the contrary, it is probably true to say that most species are as plentiful as ever, and some may even be more plentiful. It is evident that many animals find no difficulty in living and reproducing under water conditions that seem to affect some other species adversely. Nevertheless, it is possible that at least some of the former are invigorated by an *elegans* environment, and that under laboratory conditions their larvae may succeed in *elegans* water when they will fail in that obtained from another water mass. *Ophelia bicornis* is an instance of a species thriving in a non-*elegans* environment, though there is no doubt that its larvae did better in the laboratory when kept in Celtic water (which in these experiments seemed always to have been *elegans* water) than in Outside water from the Eddystone region. It should be noted that *Ophelia* larvae have not been tested with the inshore estuarine water of their natural environment, which may well be more suitable for them than Outside water.

## SUMMARY

Eggs and larvae of *Echinus esculentus*, *Ophelia bicornis* and *Sabellaria alveolata* developed abnormally, or were in poor health, in sea water collected from the English Channel in the region of the Eddystone, although in water collected from the Celtic sea development was generally normal and healthy. Experiments indicated that the Channel water lacked some unknown constituent, essential for healthy development of these species, present in the Celtic sea. The results accord with some of the hydrographical and biological changes in the area which have taken place within recent years.

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## EXPLANATION OF PLATES

(All photographs on both plates are by electronic flash at about $\frac{1}{5000}$ sec.)

### Plate I

Fig. 1. Normal swimming plutei from Celtic water, Exp. 5. Photographed alive on 7. iv. 50 when 8 days old, × 43.

Fig. 2. Abnormal swimming plutei from Outside water, Exp. 5. Photographed alive on 7. iv. 50 when 8 days old, × 43. At this time no normal plutei were present in any of the Outside water dishes. Many lying on the bottom were in worse condition than these.

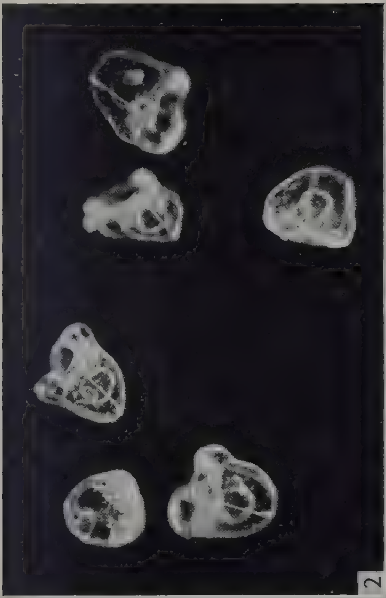
Fig. 3. Normal plutei from Celtic water, Exp. 8 A. Larvae in Celtic water in Exp. 8 B were indistinguishable from these. Photographed alive on 8. v. 50 when 3 days old, × 25.

Fig. 4. Abnormal plutei from Outside water, Exp. 8 A. Larvae in Outside water in Exp. 8 B were indistinguishable from these. Photographed alive on 8. v. 50 when 3 days old, × 25.

### Plate II

Fig. 1. Typical dishes from Exp. 8 A photographed on 9. v. 50 when the larvae were 4 days old. On the left is an Outside water dish with most of the larvae concentrated in a patch on the bottom, although a fair number are still swimming in mid-water. The other four Outside water dishes were similar. On the right is a Celtic water dish with all the larvae swimming well up. The other four Celtic water dishes were similar.

Fig. 2. Typical dishes from Exp. 9 photographed on 16. v. 50 when the larvae were 6 days old. The Berkefeld filter candles had been changed over since Exps. 8 A and B (see p. 12). On the left is a Celtic water dish with many larvae swimming well up although some are resting on, or are close to, the bottom; few are dead. The other Celtic water dish was similar. On the right is an Outside water dish with almost all the larvae dead in a large patch on the bottom. The other Outside water dish was similar.



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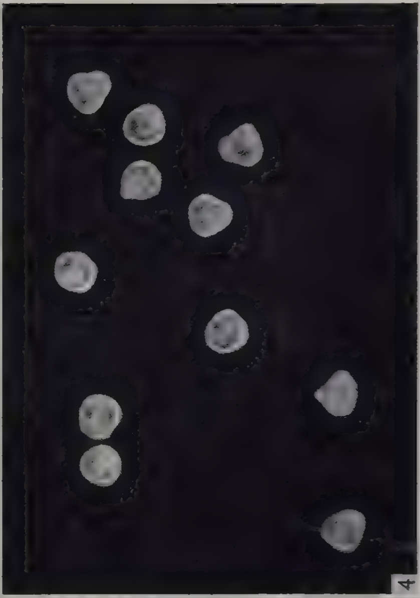

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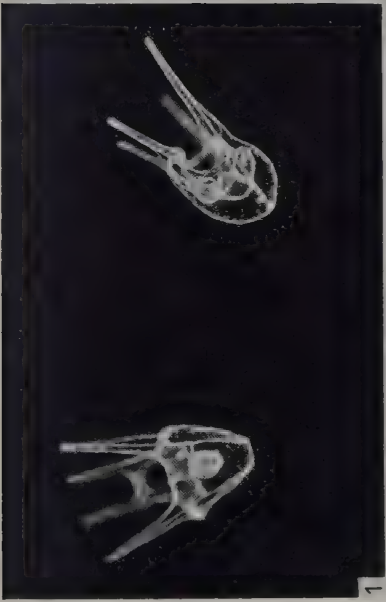

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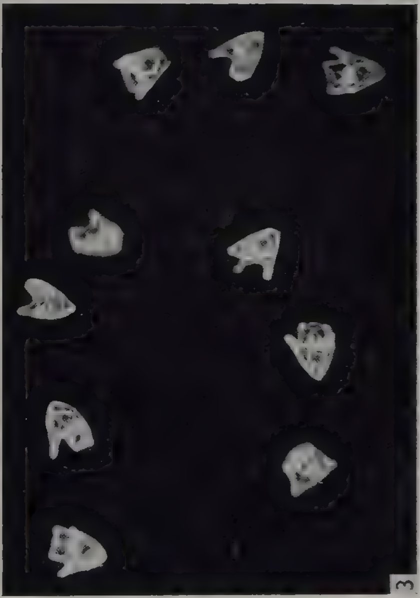

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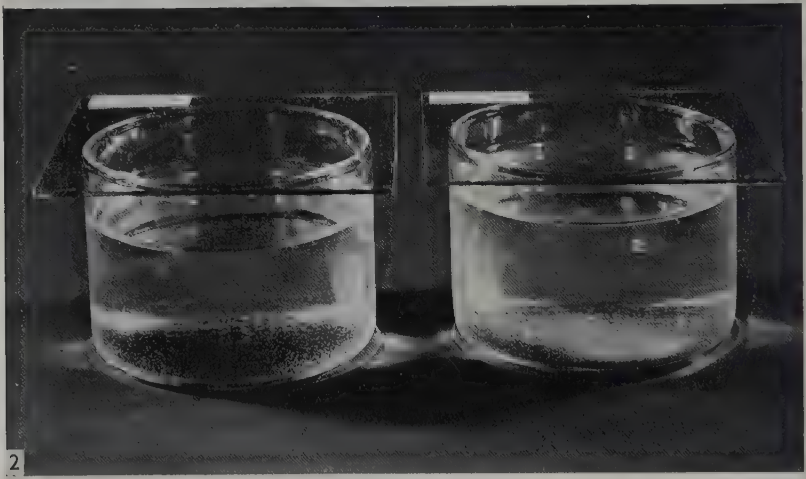


2

# CHEMICAL PROPERTIES OF THE SEA WATER IN THE NEIGHBOURHOOD OF THE LABADIE BANK

By L. H. N. Cooper, D.Sc., F.R.I.C.

Chemist at the Plymouth Laboratory

(Text-figs. 1–3)

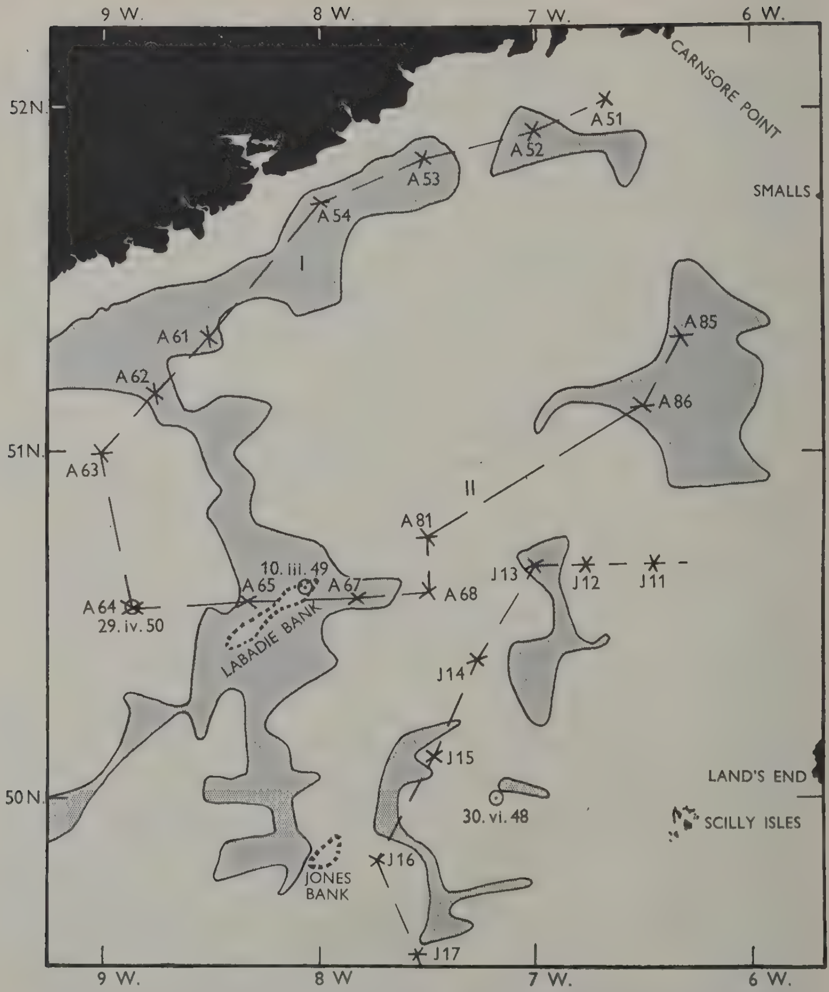
A number of excursions to the Celtic Sea have been made, first, to obtain for Dr D. P. Wilson water as contrasted as possible with that in the English Channel near Plymouth, and secondly to obtain answers to hydrographical queries. This paper presents some of the chemical findings which may prove to be relevant to Wilson's investigations on the development of the young planktonic stages of invertebrates. Since not all sea water in the Celtic Sea was likely to be equally suitable for his work, some means was needed for quickly assessing waters on the spot. There are a number of objections to the use of phosphate or other chemical analyses on board so that examination of plankton hauls was chosen. Suitable water was selected on the basis of the bulk and variety of zooplankton and the presence of species known to indicate '*elegans*' water. The 2 m. stramin ring-trawl, fished for the standard half-hour oblique haul, was used.

On the earlier cruises the water was sampled at the surface with a wooden bucket and filled into carboys through a wooden funnel fitted with a 200-meshes-to-the-inch silk strainer. The occasional high values for phosphorus compounds and iron found in surface water suggest that various kinds of dross may accumulate there so that, in the later work, collection was made from 20–30 m. depth through a rubber hose. This water did not pass through the pump used.

All carboys were very well cleaned by Mr F. A. J. Armstrong personally, using water-white technical grade sulphuric acid, followed by Plymouth tap water and plenty of distilled water. Chromic cleaning mixture was never used. The bark bung was covered with a clean piece of waterproof paper. The wooden bucket and funnel are well cared for and were vigorously swilled with sea water on the spot. Soap was never used. The rubber hose was washed out by running water through it to waste for several minutes.

'Celtic' water, shown by Wilson's experiments to promote more healthy growth and development than 'Outside' or 'Channel' water, was drawn from the following positions which are shown by circles in Fig. 1.

| Date | Lat. | Long. | General position |
|---|---|---|---|
| 30. vi. 48 | 50° 00′ N. | 7° 10′ W. | 35 miles west of Scilly Isles |
| 10. iii. 49 | 50° 36′ N. | 8° 04′ W. | Over Labadie Bank |
| 29. iv. 50 | 50° 33′ N. | 8° 51′ W. | 20 miles west of Labadie Bank (Station 64) |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6 W.
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51N.
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A62
A63
A64
29. iv. 50
A65
10. iii. 49
A67
A68
LABADIE BANK
A81
II
A85
A86
J11
J12
J13
J14
J15
J16
J17
30. vi. 48
JONES BANK
LAND'S END
SCILLY ISLES

Fig. 1. Areas of mud and ooze (stippled) in the Celtic Sea (after Laurie Norie and Wilson's chart (1919) of the Outer Grounds of the English Channel). Stations, marked by crosses, worked in April 1950 (prefixed by letter A) and in June 1950 (prefixed by letter J). Stations, marked by circles and dated, where waters for Dr Wilson's experiments (1951) were collected.

For each of these waters a description of the chemical properties has already been given in Wilson (1951, pp. 3, 5, 10).

No attempt has been made to contrast one Celtic Sea water with another. We cannot say whether waters which yielded sparse catches with the ring trawl would have caused poor development of *Echinus* and other invertebrates. The positive conclusions were: (*a*) water collected in spring over or a few miles to the west of the Labadie Bank was favourable for the development of young *Echinus esculentus*, a sea-urchin, and *Sabellaria alveolata*, a polychaete worm; (*b*) water collected at midsummer 35 miles west of Scilly was favourable for development of the polychaete *Ophelia bicornis*.

It is not yet possible to say how far these conclusions may be generalized for other seasons and other areas in the Celtic Sea. None the less, the March 1949 search for a suitable water was conducted much at random and several poor plankton catches were taken before the rich one over the Labadie Bank. In April 1950, also, suitable water was found not far away. Since other lines of evidence are pointing to the Labadie area as important in the economy of the Celtic Sea, it is proposed to report them here.

Around the Labadie Bank weak tides should facilitate the accumulation of detritus in the deeper water and the deposition of fine sediment. Much mud and ooze on the sea-bed surrounding the bank is shown on the chart of the outer grounds of the English Channel, published in 1919 by Laurie Norie and Wilson and based on Admiralty soundings with the primed lead (Fig. 1). The areas of mud and ooze are stippled. Richness of this mud in organic matter still needs to be demonstrated.

In April 1950 hydrographical stations were worked on a course laid over the bank. Due to overcast weather there is a possible error of 5 miles or so in the dead reckoning of some of the positions so that stations 68 and 81 shown as lying outside of the muddy area may actually have lain within it. It was anticipated that regeneration and breakdown of suspended detritus and of mud would be revealed by a notably higher content of total and phosphate phosphorus in the bottom water. The results confirmed the hypothesis although they did not prove it (Fig. 2).

At stations 62, 61, 53 and 52 on Section I (Fig. 2) and at station 67 on Section II (Fig. 3) which all overlay mud or ooze, the content of phosphate-phosphorus in the bottom water was relatively high. Total phosphorus was high by the same amount, providing strong confirmation of this enrichment of the bottom water. At station 81 a single analysis on the bottom water gave a high content of total phosphorus but no parallel analysis of phosphate-phosphorus was made.

At station 85 over another area of mud in the 'submerged estuary' of the 'Irish Channel River', high content of total- and phosphate-phosphorus was also observed in the deeper water. The neighbouring station 86 over mud did not show the phenomenon, whilst station 65 over mud to the west of Labadie Bank showed it only weakly.

There was no evidence of bottom regeneration of any form of phosphorus at the remaining forty-three stations worked in April 1950 over non-muddy

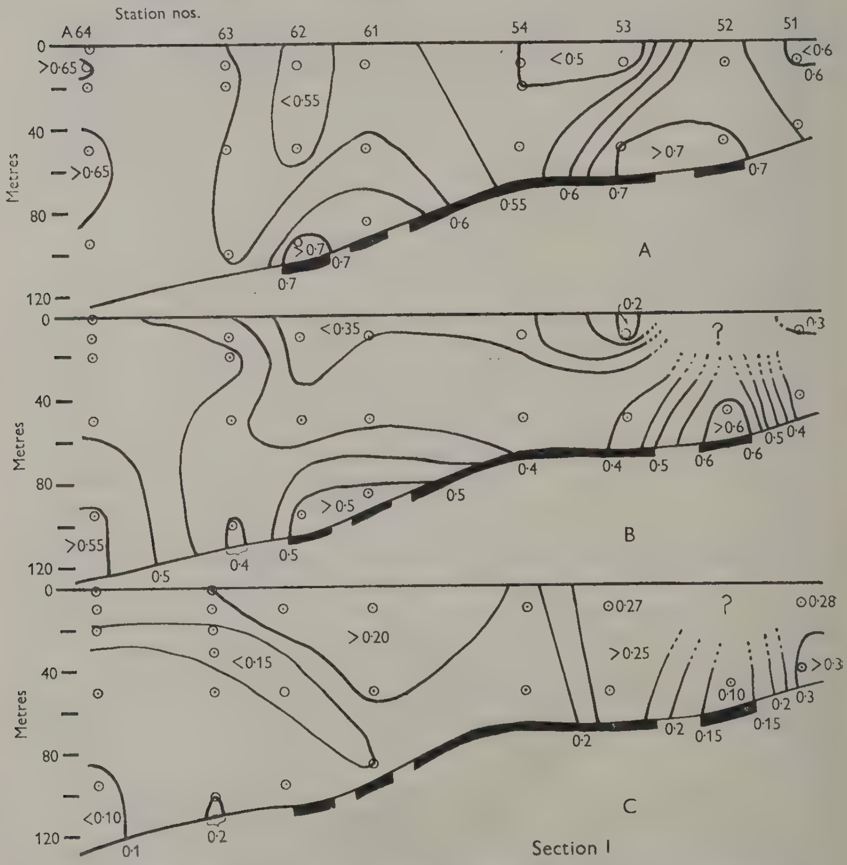

Fig. 2. Vertical Section I of stations worked over mud or ooze for (A) total phosphorus, (B) phosphate-phosphorus and (C) organic phosphorus in the Celtic Sea, 25–29 April 1950. Areas of mud and ooze are shown by thickening of the bottom lines of the sections.

bottoms. On the June cruise also there was no evidence of bottom regeneration from the non-muddy areas; the course from stations 12 to 17 (Fig. 1) lay over small muddy patches, although only one actual station was so placed. Interpretation of the small differences observed, complicated by thermal stratification, is difficult.

Enrichment of the bottom water by breakdown of suspended detritus or of ooze and mud is unlikely to be confined to phosphate. Other nutrients and growth-affecting substances are likely to accompany it. Rich catches of the larger zooplankton may be had from many parts of the Celtic Sea where a number of very different methods of enrichment are possible. None the less, it is a suggestive coincidence that two of the water samples which proved

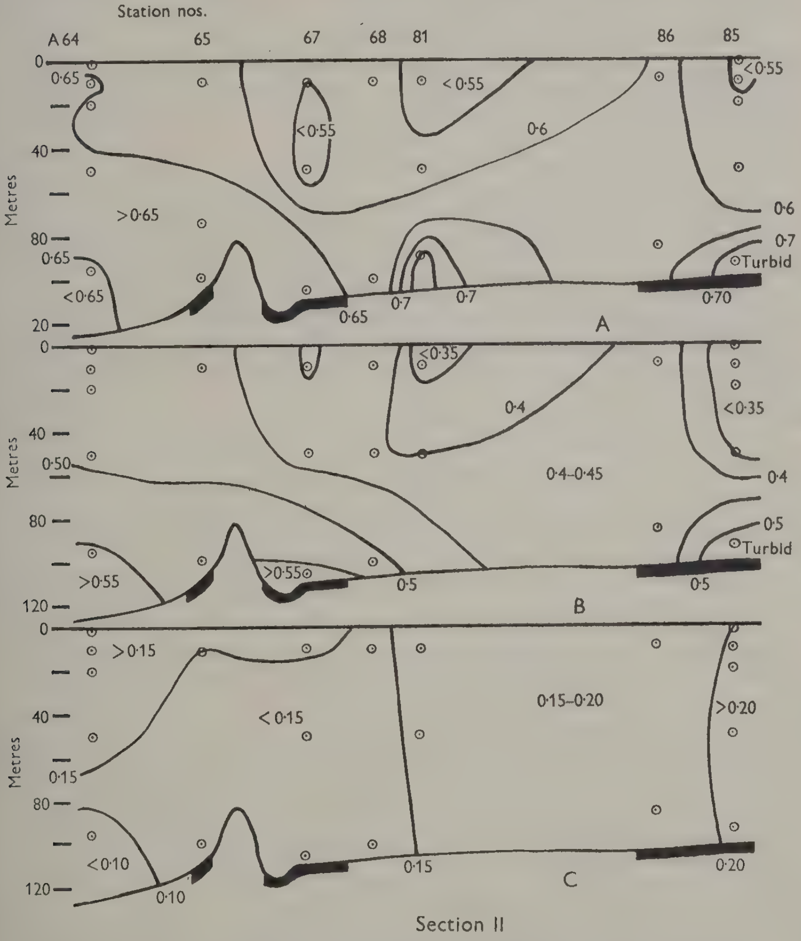

Fig. 3. Vertical Section II of stations worked over mud or ooze, as in Fig. 2.

successful in Wilson's experiments were taken in the Labadie area, where regeneration of phosphate and presumably other growth-promoting substances was occurring in the deeper water. The neighbourhood of the Labadie Bank should repay intensive study.

Thanks are tendered to Mr F. S. Russell, Dr H. W. Harvey, Mr G. A. Steven, Dr D. P. Wilson and Mr P. G. Corbin for valuable discussions, to Mr F. A. J. Armstrong who carried out all the chemical analyses and with great care prepared all the gear for sea, and to Lieut.-Cmdr. C. A. Hoodless, D.S.C., R.N.R., and the crew of R.V. *Sabella*.

## Summary

The manner of collecting water samples for Dr D. P. Wilson's experiments on a biological difference between natural sea waters has been described. Two of these samples were from the neighbourhood of the Labadie Bank.

Chemical results are presented which suggest that extensive regeneration of phosphate is occurring from the mud and ooze deposits which surround the Labadie Bank or from detritus accumulating in the deeper water due to weak tides.

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Wilson, D. P., 1951. A biological difference between natural sea waters. *Journ. Mar. Biol. Assoc.*, Vol. xxx, pp. 1–20.

# THE DEVELOPMENT AND EARLY STAGES OF THE ASCIDIAN *PYURA SQUAMULOSA* (ALDER)

By R. H. Millar
The Marine Station, Millport

(Text-fig. 1)

In the family Pyuridae the larval and post-larval stages are known only in *Halocynthia pyriformis* (Rathke) and *Boltenia echinata* (L.). Berrill (1948) has pointed out that this is the least specialized family of the Pleurogona and that its larvae are therefore of particular interest.

On 1 August 1950 specimens of *Pyura squamulosa* (Alder), up to 36 by 30 mm., were collected from boulders at low-water level in the Sound of Kerrera, Argyll. They were taken on the following day to the Marine Station, Millport, and there kept in running sea water until 4 August, when artificial fertilizations were carried out.

*Egg* (Fig. 1 A). The ripe ovum is spherical, orange-pink, and 160 $\mu$ in diameter. It is surrounded by loosely arranged inner follicle cells, a chorion, and a complete layer of rounded outer follicle cells. When the egg is freshly drawn from the ovary there is a narrow perivitelline space, but after some minutes in sea water the space is enlarged by the osmotic uptake of water and the diameter of the chorion increases from 175 to 190 $\mu$. The final external diameter of the layer of outer follicle cells is about 220 $\mu$.

*Sperm* (Fig. 1 D). The form of the sperm is typical of that of many ascidians. The rod-like head is 9 $\mu$ long and has a protoplasmic bulge near the point of attachment of the tail. The tail is a flagellum about 50 $\mu$ long.

*Fertilization and development.* The eggs and sperm from two individuals were mixed in sea water, and in spite of the alleged difficulty in obtaining fertilized eggs of pyurid ascidians (Berrill, 1950), development proceeded, and apparently normal larvae were obtained in large numbers. Cleavage follows the pattern which is now well established in ascidians. A deep orange crescent (Fig. 1 B) appears in the fertilized egg like the yellow crescent of *Styela partita* (Conklin, 1905) and the bright orange crescent of *Boltenia echinata* (Berrill, 1948); pigmentation of this kind is unknown in other ascidians. The pigment is later localized in the tail of the larva (Fig. 1 C). Most of the eggs fertilized about 11.30 a.m. on 4 August, and kept in Petri dishes at 18–19° C. had hatched as active larvae by 9.30 a.m. on the following day.

*Larva* (Fig. 1 E). The trunk of the larva is about 200 $\mu$ long and the tail about 730 $\mu$ long, inclusive of the posterior projection of the fin. There are two dorsal and one ventral anterior papillae of conical shape. The fin runs round the

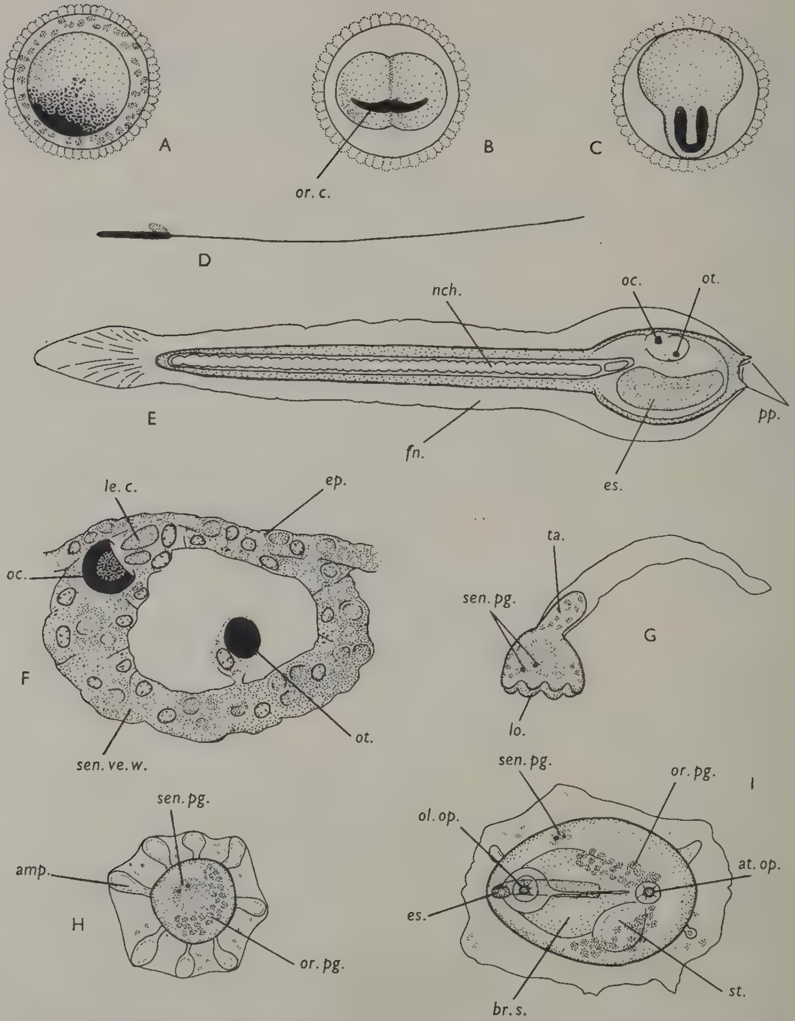
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Fig. 1. Development of *Pyura squamulosa* (Alder). A, fertilized egg showing concentration of pigment forming orange crescent. B, first cleavage, showing orange crescent. C, embryo with trunk and tail differentiated and orange pigment localized in tail. D, sperm. E, larva. F, sagittal section through larval sensory vesicle. G, metamorphosing larva. H, post-larval stage with ampullae. I, young ascidian. *amp.*, ampulla; *at. op.*, atrial opening; *br.s.*, branchial sac; *ep.*, epidermis; *es.*, endostyle; *fn.*, fin; *le.c.*, lens cell; *lo.*, anterior lobes; *nch.*, notochord; *oc.*, ocellus; *ol.op.*, oral opening; *or.c.*, orange crescent; *or.pg.*, orange pigment; *ot.*, otolith; *pp.*, papillae; *sen.pg.*, remains of larval sensory pigment (otolith and ocellus); *sen.ve.w.*, wall of sensory vesicle; *st.*, stomach; *ta.*, tail being resorbed.

trunk in the sagittal plane and bifurcates on the dorsal surface of the trunk to send a short ridge forward to each dorsal papilla. On the ventral surface of the trunk the fin remains simple and runs forward to the single ventral papilla. The rudiment of the endostyle occupies the ventral part of the trunk, and the sensory vesicle lies near the dorsal surface. Both otolith and ocellus are present and well developed (Fig. 1 F). The otolith is contained in a single cell projecting up from the floor of the sensory vesicle, and consists of a spherical or ovoid mass of black pigment. The mean value of the greatest diameter of this pigment mass is $13{\cdot}2\,\mu$. On the postero-dorsal wall of the sensory vesicle lies the ocellus. This has a cup-shaped mass of black pigment of which the mean diameter across the opening is $14{\cdot}3\,\mu$. In addition to a number of retinal cells there are, opposite to the opening of the pigment cup, three cells each containing a large clear body acting as a lens. The distal ends of the lens cells are closely applied to the lower surface of the dorsal epidermis. No trace was found of the rudiments of siphons, or peribranchial sacs. The tail has the usual single row of notochordal cells surrounded by muscle cells, and also contains the pigment which formed the orange crescent of the fertilized egg. Before the larva hatches the tail is coiled in a horizontal plane.

## METAMORPHOSIS AND POST-LARVAL DEVELOPMENT

Within 12 hr. of hatching resorption of the tail is in progress both in larvae attached to the glass of the vessel and in those unattached (Fig. 1 G). At the same time the trunk becomes shorter and wider. Eight lobes now appear round the anterior margin of the trunk, and the tail begins to shorten; the test round the tail, however, is not resorbed. By the time the tail has disappeared the eight anterior lobes have developed into eight ampullae growing out laterally over the substratum. At this stage two black pigment spots represent the remains of the larval otolith and ocellus, and the orange pigment from the larval tail forms a band across the body of the young ascidian (Fig. 1 H). Later the ampullae become irregular in outline and constricted at the base, and soon some of them disappear. At about this time the endostyle becomes clearly visible. At the next stage the functional ascidian is recognizable, having oral and atrial openings, active body musculature, branchial sac with protostigmata, and stomach containing food masses (Fig. 1 I). The ampullae are represented by one or two small irregular projections from the basal part of the body. The remains of the larval otolith and ocellus show as two black spots on the right side of the body, and not, as found by Berrill (1929) in *Halocynthia pyriformis*, near the adult ganglion.

Subsequent development was not followed, as all the major changes in organization from larva to adult were now complete.

The development time-table is given below.

4 August: 11.30 a.m., fertilization; 1.00 p.m., 1st cleavage; 2.30 p.m., 4th cleavage; 3.30 p.m., 5th cleavage; 5.00 p.m., gastrulation; 6.00 p.m., deep gastrula; 9.00 p.m., differentiation of trunk and tail. 5 August: 9.30 a.m., hatching of larvae almost complete; 7.30 p.m., tail resorption in progress. 7 August: tail completely resorbed; ampullae well developed. 8 August: diameter of post-larva over ampullae 0·33 mm. 10 August: diameter of post-larva over ampullae 0·40 mm. 11 August: diameter of post-larva over ampullae 0·48 mm. 14 August: oral and atrial openings, branchial sac and gut differentiated. 17 August: feeding first observed.

The temperature from the time of fertilization until the end of tail resorption was 18–19° C. and thereafter 23° C.

In Table I some of the important features in the development of *Halocynthia pyriformis*, *Boltenia echinata* and *Pyura squamulosa* are compared.

TABLE I

| | *Halocynthia* | *Boltenia* | *Pyura* |
|---|---|---|---|
| Pigmented crescent in developing ovum | 0 | + | + |
| Diameter of ovum (mm.) | 0·26 | 0·18 | 0·16 |
| Larval sense organs | Otolith and ocellus | Otolith and ocellus | Otolith and ocellus |
| Number of lens cells in ocellus | 3 | 3 | 3 |
| Rudiments of peribranchial sacs in larva | + | + | 0 |
| Number of ampullae in post-larva | 4 | 4 | 8 |

The Pleurogona (= Stolidobranchiata Lahille, 1886) comprises the families Styelidae, Pyuridae, and Molgulidae. In these families the sensory equipment of the larva is variously modified or reduced. Thus the ocellus has disappeared in the larvae of all the Molgulidae, the most highly developed of pleurogonid ascidians. In the Styelidae the ocellus may be combined with the otolith (subfamily Botryllinae), or absent (Dendrodoa, Polycarpa), or merely reduced (Styela). The larvae of the Pyuridae have hitherto been known only from *Halocynthia pyriformis* and *Boltenia echinata*. In both of these the ocellus is present and of normal structure (Berrill, 1950), though not so well developed as in the larvae of the enterogonid ascidians.

In *Pyura squamulosa* the larger size of the ocellus represents a more primitive condition. The larva is also less specialized in that it shows no trace of precociously developed peribranchial sacs or siphon rudiments such as those of *Boltenia*. It is indeed nearer to the enterogonid type of larva than that of any other known pleurogonid ascidian. The small size of the egg also indicates a condition at least as primitive as *Boltenia* and considerably more primitive than *Halocynthia*. The presence of a pigmented crescent in the developing egg of *Pyura squamulosa* and *Boltenia* suggests that these forms may be closer than *Halocynthia* to the styelid stock, at least one member of which shows a similar pigmented crescent.

Evidence gained from a study of the development of *Pyura* therefore indicates it to be more primitive than either *Boltenia* or *Halocynthia*, the other two pyurid ascidians whose development is known.

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# *CORELLA HALLI* N.SP., A NEW ASCIDIAN FROM THE ENGLISH CHANNEL

By Patricia Kott, M.Sc.[1]

From the Plymouth Laboratory

(Text-fig. 1)

In September 1950 Dr H. W. Parker of the British Museum (Natural History) kindly sent me a specimen of an ascidian collected by the yacht, *Manihine*, for identification. This has proved to belong to an unnamed species of the genus *Corella*, here described as *C. halli*. The unique type specimen was obtained from dredgings on a shingle bottom at 35 fathoms, 10 miles WSW. of the Casquets in the English Channel, 30 August 1950 (*Manihine*, Station no. 81).

*External features*. The animal (Fig. 1A) is enclosed in a transparent test, laterally flattened, circular, of 4 mm. diameter and fixed basally to pieces of sand; there is no stalk. The branchial aperture is terminal anteriorly; the atrial aperture is also anterior and dorsal to the branchial aperture. Both apertures are sessile.

*Mantle*. The animal inside the test is 2 mm. in diameter. The mantle musculature is weakly developed (Fig. 1B): there is one circular muscle band around the base of each siphon, five narrow muscle bands run transversely across the anterior aspect of the body ventral to the branchial siphon, another five bands radiate from each side of the branchial siphon and two similar bands radiate from the atrial siphon. In the postero-dorsal corner of the left side of the body there are seven narrow bands of muscle set obliquely.

The atrial siphon is bordered by six small pointed lobes and the branchial siphon has eight similar lobes.

*Tentacles*. The branchial tentacles are simple; there are fifteen long slender tentacles alternating with the same number of very short tentacles.

*The dorsal tubercle* (Fig. 1C) is anterior and to the left of the neural ganglion and slightly on the left side of the peritubercular prebranchial space. It is of the usual semicircular form typical of this genus, with the concavity directed anteriorly and to the right.

*Dorsal lamina* (Fig. 1C). Languets representing the dorsal lamina are short, broad laterally, and flattened antero-posteriorly. Terminally they come to a sudden small point and are not long and tapering as are the dorsal languets of *C. parallelogramma* (Müll.). In this specimen there are eleven languets.

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*Branchial sac.* The form and arrangement of the stigmata (Fig. 1 D) are similar to those found in immature specimens of *C. parallelogramma*: the stigmata are arranged in pairs in fourteen transverse rows. There are twenty longitudinal vessels on each side of the body supported by papillae between each of the stigmata; intermediate transverse vessels are present and these occasionally carry a small papilla between two successive longitudinal vessels. The anterior and posterior corners of the stigmata of each pair are turned inwards and in the posterior part of the sac there are still a few stigmata joined in the horizontal plane (Selys-Longchamps, 1901, pl. XXIV, fig. 7).

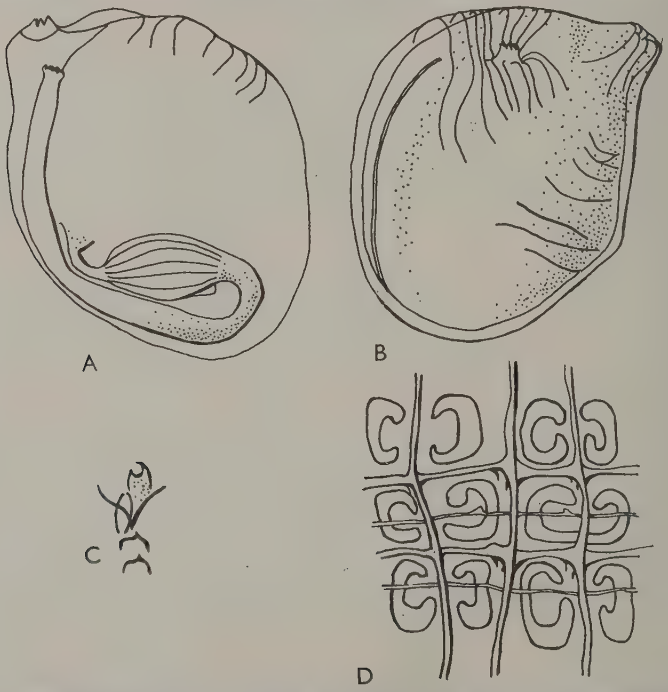

Fig. 1. *Corella halli* n.sp. Type specimen. A, zooid from the right side showing alimentary canal, ×24; B, zooid from the left side showing mantle musculature, ×24; C, region of the neural ganglion showing the anterior part of the dorsal limina, the dorsal tubercle and neural ganglion, ×72; D, part of the posterior end of the branchial sac showing one pair of the stigmata joined in the horizontal plane, ×72.

*Alimentary canal* (Fig. 1 A). The oesophagus is short and narrow and opens into a spindle-shaped stomach with twelve longitudinal furrows and a short pyloric caecum. The anal opening is fringed by eight rounded lobes. The alimentary canal is completely on the right side of the body.

*Gonads.* Gonad cells are present and spread diffusely over and between the loop of the alimentary canal as in other species of this genus.

*Relations.* In the form of its branchial sac this specimen might be identified as a young specimen of *C. parallelogramma* (Müll.); it is here described as a new species, however, since there are certain distinctive features which do not occur in *C. parallelogramma* and since the presence of gonad cells indicate a mature form. The species is distinguished from *C. parallelogramma* by the following characters: the tentacles are of two orders, long alternating with very short; the alimentary canal is on the right-hand side of the body, whereas in the young forms of *C. parallelogramma* which have been described the alimentary canal is posterior to the branchial sac; the stomach is longer and more spindle-shaped and there are lobes present around the anus while the anal borders of several specimens of *C. parallelogramma* examined are smooth; the languets of the dorsal lamina are fewer. Unless further collection and study of the development of *C. parallelogramma* indicates that this specimen is merely an individual variant of a young form, the species is particularly interesting and shows a primitive condition of the branchial sac in the evolution from straight to coiled stigmata. It is natural to assume that there may be some species in the transition stage which the form described above would represent; a stage in the evolution of *Corella* which is recapitulated in the life history of the more highly specialized *C. parallelogramma*.

*Corella halli* n.sp. is named after Major H. W. Hall, M.C., who has made his yacht *Manihine* available to the British Museum for collecting; the specimen comes from the *Manihine* collections of the British Museum (Natural History) where it is deposited under the type number B.M. 1950.9.21.1. My thanks are due to Dr H. W. Parker for giving me the opportunity of describing it.

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# *TURBONILLA ELEGANTISSIMA* (MONTAGU), A PARASITIC OPISTHOBRANCH

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(Text-figs. 1–2)

*Turbonilla elegantissima* (Montagu), though one of the larger and more familiar members of the family Pyramidellidae, is known only by the shell and the appearance of the animal when crawling. Forbes & Hanley (1853) and Jeffreys (1867) state that it is common around the British Isles, and that its foreign distribution is from Tromsö to the Mediterranean. In the fauna list of the Marine Biological Association (1931) it is recorded as *T. lactea* (L.) 'occasionally under stones, particularly where there is a certain amount of silt' from low water to a depth of 10 fathoms, and, in the Salcombe estuary, 'very common on the Zostera south of Pilworthy Pt., (Allen & Todd, 1900)'. Actually this opisthobranch has its own extremely specialized habitat, as do, apparently, all other members of its family (Fretter & Graham, 1949): like them it is an ectoparasite, restricted to the vicinity of its host. Specimens have been collected from the laminarian zone along the south coast of Devon and Cornwall, the largest number from Church Reef, Wembury, where silt and sand around boulders and between shale ledges provide suitable niches for such sedentary worms as *Audouinia tentaculata* and *Amphitrite gracilis*. When covered by the tide the tentacles of these polychaetes extend through the silt and sand and spread over the surface of the rocks for a considerable distance, and it is in the vicinity of these tentacles that *Turbonilla* lurks to suck liquids from them by means of a long proboscis (Fig. 1). *Audouinia* and *Amphitrite* were also recorded at Pilworthy Pt., but their association with *Turbonilla* was then unknown. When the laminarian zone is uncovered the mollusc may wander some distance from its host, in a more superficial position on the shore, clinging to the half-buried stones or just hidden by the silt. It has never been collected from exposed sandy shores, which might offer a suitable habitat for the host, but no safe crannies for the protection of the parasite. Thus *Turbonilla* burrows to seek its food, and in this respect differs from the *Odostomia* spp. which have been described (Fretter & Graham, 1949), for they rest on or near the entrances of the tubes of tubicolous worms, and when they feed the extending proboscis is directed upwards through the water, free of contact with the mentum beneath it, arching over in a U-shaped bend to reach the tissues of the host. *Turbonilla*, by contrast, is subterranean, ploughing its way forwards in search of food and, on sensing it, thrusting out a stout proboscis which is supported by the mentum (M) and pushed through the silt to reach the host. When the feeding process of *Turbonilla* has been observed in the laboratory the proboscis has been seen to suck blood from the tentacles of *Audouinia*, even a solitary writhing tentacle fragmented from the worm being pursued and sucked, whilst, if *Amphitrite* be the prey, either tentacles or gills may be attacked. On no occasion have I seen the proboscis fix itself to the body wall to pierce the worm: presumably this is too stout for penetration to occur.

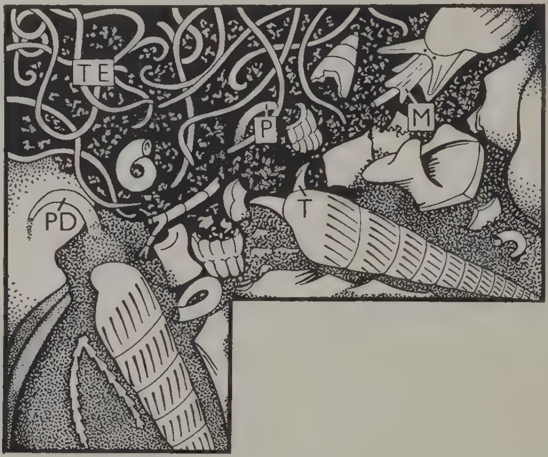

Fig. 1. *Turbonilla elegantissima* feeding on tentacles of *Audouinia tentaculata*. × 7. M, mentum through which proboscis is everting; P, proboscis sucking tentacle of *Audouinia* –its base is buried in silt; PD, retracting proboscis—detritus leaves it as it retracts; T, tentacle of *Turbonilla*; TE, tentacle of *Audouinia*.

The differences between the structure of *Turbonilla* and *Odostomia*, some of which may be correlated with the differences in habit, will be emphasized in the following description.

The slender shell, so easily pulled through the silt, is too long to be held erect when the mollusc comes to the surface and creeps along the shore, and it is then dragged awkwardly behind the short foot. The exposed parts of the body are white and, as in closely related opisthobranchs, are withdrawn into the calcareous shell and shielded by the operculum when the animal is disturbed. The operculum is orange and lacks the teeth which in *Odostomia* project into the flesh of the foot. The foot is truncated in front, the antero-lateral corners slightly emphasized, and posteriorly it tapers to a blunt point. The sole is covered with columnar epithelium, strongly ciliated, and the same epithelium spreads over the upper surface of the propodium to surround the opening of the anterior pedal mucous gland, and covers the dorsal surface of the mentum. Elsewhere over the foot cilia are more infrequent. The mentum (Fig. 1, M) is a rectangular outgrowth from the foot, narrow in the transverse plane, and it lies between and beneath the tentacles. It differs from the mentum of *Odostomia* in that the introvert, instead of opening above it, extends through it and opens subterminally on the dorsal surface by an inconspicuous aperture. The introvert opens in the same position in *Turbonilla jeffreysii*. A median longitudinal furrow runs along the dorsal surface of the mentum above the introvert, and extends to the tip, that is, beyond the mouth. The furrow is lined by cuticularized cells. When the proboscis is to be used the mentum is extended in the direction of the food and held taut, and while the proboscis is gradually everting and pushing through the sand the antero-lateral corners of the tip of the mentum may be pressed against the substratum to give support.

Within the tissues of the foot, and spreading into the haemocoel of the head anterior to the nerve ring, are large numbers of mucous cells. Their contents are discharged by ducts passing between the epithelial cells of the foot. Such cells comprise the anterior pedal gland which opens on the dorsal surface of the propodium. A second large grouping discharges to the entrance of the penial sheath situated beneath the mentum, and a third, more diffuse, lubricates the surface of the sole especially the posterior half. Another type of gland cell is found within the foot forming on each side a lateral glandular streak as in *Odostomia* and in *Patella* (Yonge, 1947). Each cell is spherical, filled with globules responding to basic stains and surrounded by a lattice of muscle fibres which may help to discharge the secretion. The epithelium along the sides of the foot, on to which the ducts of these glands discharge, has scattered cells bearing bundles of long cilia; these may be sensory in nature. Similar cells are also found on the ventral surface of the mentum which is otherwise free from cilia.

The head bears a pair of black eyes closely set between a pair of tentacles (Fig. 1, T). The latter are of the typical pyramidellid type, shaped like the ears of a rabbit with a concave outer surface, though freely movable so that the concavity may face in a variety of directions. Invariably when the mollusc is burrowing and the tentacle is pressed back the concavity is lateral; the anteriorly directed surface which is pushed through the silt and sand is thickly ciliated, the cilia directing particles towards the tip. These cilia, together with those on the propodium and the dorsal surface of the mentum, form a cleansing current which sweeps sand and silt posteriorly over the head and out to each side. The posterior surface of the tentacle is not ciliated except for the rim bordering the concavity, and the epithelium of the concavity has only scattered tufts of cilia; these may be sensory. The tentacles of *Odostomia* are held erect when the mollusc is active, perhaps to sample the water, or to sense currents in its vicinity: this function would appear to be less significant in *Turbonilla*, which also lacks the ganglionic mass in the core of each tentacle.

The mantle cavity is deep and narrow. From it have disappeared the osphradium and ctenidium, and the opening of the hermaphrodite duct has been removed to a more anterior position. The rectum and kidney discharge into the posterior half. The anus is on the floor at the posterior end on the extreme right side, and the renal aperture is on the roof at the apex of a papilla which is at the anterior end of the kidney, about halfway along the mantle skirt, slightly to the left of the median line. The kidney lies wholly within the mantle skirt, occupying the posterior half of the left side, and its blood drains to the large efferent pallial vessel which courses along the left wall of the kidney to the auricle. A low, cubical, or even squamous, epithelium lines the greater part of the mantle cavity and permits ready exchange of respiratory gases between the water in the cavity and the blood vessels in the mantle skirt. Beneath this epithelium along the right wall is a strip of gland cells arising near the anus, which broadens as it passes anteriorly. Here the gland cells become larger and fewer. There appear to be two types of cell comprising this strip: one, the larger, elaborates secretory masses of irregular shape which stain deeply at first with iron haematoxylin, but near the time of liberation stain less intensely; whilst the second is filled with granules shaped like rice grains and always staining deeply with basic dyes. The secretion from these glands presumably helps to lubricate the passage of the faeces, supplementing the meagre secretion from the short intestine. On entering the anterior half of the mantle cavity the glandular strip leaves the mantle skirt and passes ventrally to the dorsal wall of the body along which it runs, first to the right of the pallial hermaphrodite duct and then above it.

The anterior half of the mantle cavity contains two important structures: the hypobranchial gland, which spreads along the roof anterior to the kidney and approaches the pallial edge, and, along the right wall, an exhalant gutter which is extended anteriorly beyond the mouth of the shell into a spoon-shaped siphon. The gutter arises anterior to the point at which the strip of subepithelial gland cells, running forwards from the anus, passes medially on to the body wall. It is bordered on either side by a narrow strip of tall columnar epithelium, about a dozen cells broad, which is covered with long, closely set cilia. Between these bands the epithelium contains brown pigment granules and is not ciliated. One band runs along the mantle skirt on its extreme right side, and the other lies on the body wall immediately beneath it keeping to the right of the genital duct. Posteriorly the two converge and unite. The effective stroke of the cilia directs particles mixed with hypobranchial secretion forwards into the exhalant channel. The same general arrangement of this cleansing path from the mantle cavity is found in *Odostomia* (Fretter & Graham, 1949) and also in *Omalogyra* and *Rissoella* (Fretter, 1948); it appears more important in *Turbonilla*, and, while the animal burrows, a rope of detritus adhering to secretion is poured from the mantle cavity by its activity. In all of these gastropods gill filaments have been lost, and their function of maintaining a stream of water through the mantle cavity is taken over by the ciliated strips of columnar epithelium along the exhalant path; the vascularized mantle skirt takes over the respiratory function of the gill.

At the anterior edge of the mantle skirt the epithelium is columnar, and in the pallial thickness is a complicated musculature and many mucous glands which discharge on to the surface.

In *Odostomia* the opening of the hermaphrodite duct is just within the mantle cavity, and from it a ciliated tract directs spermatozoa around the base of the right tentacle to the penial sheath. In *Turbonilla* the pallial duct is extended forward in the direction of the ciliated tract and opens on the propodium in front of the right tentacle and to the right of the mentum: in fact the common genital aperture is anterior to the opening of the penial sheath. Yet another opening lies on the side of the head, just behind the genital one and slightly more median. It is the duct of a muscular pouch which lies in the haemocoel and may be associated with the genital system.

Differences between the alimentary canal of *Turbonilla* and *Odostomia* are for the most part insignificant. The acrembolic proboscis grips the tentacle of the host with a sucker, formed from modified lips, and the piercing action of the stylet is synchronized with the attachment. The stylet is short, occupying only one-tenth of the length of the fully extended proboscis as compared with one-third in *Odostomia*; such a short stylet is not found in *Turbonilla jeffreysii*, an ectoparasite of hydroids and the only other member of the genus which has been studied. As in this species, however, and in contrast to *Odostomia*, the oral tube is not divided into a dorsal channel for the stylet and a ventral food channel: the sucker surrounds a single opening through which the stylet protrudes and into which the food is drawn. The cuticle comprising the stylet is secreted from the dorsal wall of the oral tube, like the jaws of more unspecialized gastropods. It extends forwards to embrace, and to envelop anteriorly, a projection arising from a more posterior part of the dorsal wall of the oral tube and passing through it to the sucker. This projection, forming the core of the stylet, contains the fused salivary ducts which open at the tip of the spike, and must pour secretion into the wound inflicted by it. Posteriorly the median salivary channel enlarges to a club-shaped origin, a region that invariably contains some saliva. Its walls are thickened by a complexity of muscles in which are embedded the ends of the salivary ducts and which are responsible for the movements of the stylet.

The oral tube has a low cubical epithelium which turns outwards over the sucker to meet the epithelium of the introvert; only at the periphery of the sucker is the epithelium ciliated. The ciliated cells, forming a ring not more than a dozen cells broad, flick particles away from the mouth as the proboscis is pushed through the silt. The intrinsic musculature of the sucker is arranged as in *Odostomia*, though the longitudinal fibres, attached at their outer ends to the underside of the epithelial cells, are longer, giving the sucker a greater depth. This muscular region is followed by a short section of the tube in which there are large subepithelial glands discharging their secretion into the lumen; in their detailed structure these resemble glands which occur in the long oral tube in *Turbonilla jeffreysii* (Fretter & Graham, 1949, fig. 5). The buccal pump arises from the ventral wall of the tube at about two-thirds of its length from the anterior end. Its low, cuticularized epithelium overlies a thick wall composed chiefly of radial muscle fibres with antagonistic transverse fibres. This musculature sets up a rhythmical pumping action when the parasite is feeding. The pump is small as compared with that of *Odostomia*, lies hidden beneath the oral tube and has no caecum; its size may be correlated with the shortness of the oral tube. All its contractile cells contain groups of fibrillae which are striated. There are some mucous cells in and under the epithelium at the posterior end of the pump, especially around its opening to the oesophagus which is on a small papilla projecting into the narrow oesophageal tube.

The epithelium of the introvert is not complex as in other pyramidellids. It is columnar and cuticularized, showing no regular papillation. In the living tissue two types of subepithelial gland cell can be distinguished: in one the cytoplasm contains colourless spherules and in the other it appears as a granular fluid of homogeneous consistency. Occasionally these gland cells occur in the epithelium. Circular muscle fibres constituting a coat of considerable thickness lie directly beneath the epithelium, and then come the longitudinal muscles which are responsible for the retraction of the extended proboscis. They take the same course as the retractors of the proboscis of *Odostomia*. As the proboscis is retracted small particles of detritus and diatoms are frequently drawn in with it (Fig. 1, PD): on its protrusion they fall off the smooth surface or are scraped off as it pushes through the substratum. The eversion of the proboscis is mainly brought about by the hydraulic action of the blood in the cephalic haemocoel. To provide for the disturbances in the vascular system which such profound changes in shape of the anterior part of the body must entail the arrangement of this system is modified to what must be regarded as the typical pyramidellid plan. A single aorta arises from the ventricle and passes up the visceral mass to open into haemocoelic spaces. The anterior aorta has no direct connexion with the heart, but runs between a vast haemocoelic sinus which bathes the pericardium and adjacent reproductive organs, and the haemocoelic spaces of the head and foot. Blood will flow anteriorly through the aorta when the proboscis is thrust out, and when it is withdrawn may be forced back In this way the reverse direction to fill the posterior haemocoelic reservoir. rapidly in injury to the heart by the sudden pressure of returning blood is prevented.

In *Odostomia* the large buccal ganglia are situated at the anterior end of the buccal pump which is regarded as part of the modified buccal cavity, the tube of capillary dimensions which leaves the pump being the oesophagus. In *Turbonilla* the ganglia are more posterior and lie near the point at which the salivary ducts leave their glands. This point may appear half-way along the muscular tube which connects the pump with the stomach, though when the proboscis is in use the part of the tube posterior to the ganglia may be extended to twice or even thrice the length of the anterior section. With the extreme specialization of the anterior part of the alimentary canal in the pyramidellids the buccal ganglia may shift from their original position. In *Cerithiopsis tubercularis* (Fretter, 1951), which shows modifications associated with a much less specialized type of proboscis, the ganglia lie at the posterior end of the anterior oesophagus where the salivary ducts leave the haemocoel and penetrate the musculature of the oesophagus within which they make their way to the buccal cavity. A similar course is followed by these ducts in *Turbonilla*. The region of the alimentary canal between buccal pump and buccal ganglia may, therefore, be regarded as the anterior oesophagus. It is a long muscular tube of uniform diameter which lies in tangled coils in the haemocoel when the proboscis is retracted, and is carried out into the proboscis when it is everted. The section of the oesophagus behind the buccal ganglia is of uniform structure throughout, and is only distinguishable from the anterior part by its musculature. The oesophageal epithelium is similar from one end to the other, being composed of low columnar cells.

The intrinsic muscles of the anterior oesophagus constitute a coat of circular fibres beneath the basement membrane of the epithelium, and an outer coat of longitudinal fibres; the salivary ducts run just within the latter. These muscles set up a peristaltic movement which can be seen when the living animal is dissected. In the wall of the posterior part of the oesophagus there are no circular muscles: its whole movement is controlled by a complex arrangement of longitudinal fibres grouped into compressed sheets which lie radially with respect to the lumen; the nuclei of the muscle cells border the haemocoel. Only the anterior part of this section of the oesophagus is drawn out into the proboscis.

Each salivary gland consists of a narrow tube, ciliated and surrounded by subepithelial gland cells except at the innermost end where the lumen swells into a thin-walled bladder lined by cubical cells without cilia. Strands of muscle attach this bladder to the wall of the posterior part of the oesophagus. The gland is connected to the stylet by a long duct which leaves its anterior end and, after a very short course in the haemocoel, passes into the intrinsic longitudinal muscles of the anterior oesophagus. The duct appears minute in transverse section, with three low epithelial cells surrounding the lumen and beneath these muscle cells containing circularly running fibrillae. Anteriorly the two ducts leave the oesophagus and pass dorsally to enter the median salivary channel which lies within the stylet. Most of the secreting cells of the gland have a similar appearance—very finely vacuolated cytoplasm which stains lightly with basic dyes and also with stains specific for mucus. The nuclei are relatively enormous and have many granulations and three or four nucleoli. There may be, as in *Odostomia*, a holocrine secretion occurring without a restitution phase: there is evidence from the appearance of the gland that new cells are formed only at the innermost end, near the terminal bladder, and spent cells, destroyed after secreting, are restricted to the region at the beginning of the duct.

When the proboscis is withdrawn the muscles of the posterior half of the oesophagus contract, shortening and broadening that tube, which comes to rest beneath the coiled anterior oesophagus and just above the columellar muscle. Posteriorly the oesophagus opens to the stomach, which is ill-defined except for its anterior wall, and which cannot elsewhere be distinguished from the digestive gland. The anterior wall is made of a small area of columnar epithelium which surrounds the oesophageal opening and the opening of the intestine lying above this. Thus the food, which is liquid and so needs no mechanical treatment before it can be absorbed, is passed from the oesophagus directly to the cells of the digestive gland; in these cells it appears, at first, in the form of brown spherules. The only waste matter which is seen in the intestine is derived from the digestive cells of the digestive gland, and is in the form of small yellow and green concretions. The intestine passes from the stomach directly to the upper end of the mantle cavity. The epithelium is ciliated and has a few scattered gland cells in which secretion spherules stain readily with basic dyes.

The important dissimilarities between the hermaphrodite reproductive systems of *Odostomia* spp. and *Turbonilla elegantissima* concern the length of the pallial duct and the organs of copulation. Perhaps of less significance are other divergent characters which are related to the accessory glands, both albuminous and mucous, and the histology of the pallial duct.

The gonadial channel which links the hermaphrodite gland with the pallial duct receives, in *Turbonilla*, a single duct which drains both the albumen and mucous glands. These glands, lying in the upper visceral coils, have, in *Odostomia*, separate ducts which converge on approaching the gonadial duct so that their openings to it are set very close together. The ducts have apparently fused in *Turbonilla*. A second mucous gland occurs in *Odostomia* and surrounds the upper end of the pallial duct, where the body broadens to its last coil, and when the female system is mature this gland spreads half-way along the duct. In *Turbonilla elegantissima* the distal mucous gland is confluent with the proximal one: a single gland, lobed and presumably not entering the last coil, has one outlet to the genital duct and a second, by a broad secretory channel, to the innermost end of the pallial duct.

The pallial duct extends on to the propodium and has, for more than half its length, an epithelium of tall columnar cells bearing long cilia. This distal region of the duct is very muscular. Elsewhere the ciliated cells lie between gland cells swollen with secretion. The gland cells are of three principal types. The most important, occurring in the centre of the secreting area and—a few—at the proximal end of the duct, contains large spherules of mucus; distally, between these and the ciliated part, and sometimes scattered amongst the mucous cells, are glands with smaller secretion globules which stain deeply with basic dyes; whilst at the proximal end of the duct the secretion within the cells, again in the form of spherules, is not mucus and stains with basic dyes only lightly. Surrounding the opening of the gonadial duct is yet another type of gland cell: the enormous nucleus is probably indicative of intense metabolic activity; the spherules of secretion stain deeply (iron haematoxylin) during their period of elaboration, but lightly near the time of liberation. This varied histological structure of the duct contrasts with the uniformity in *Odostomia*.

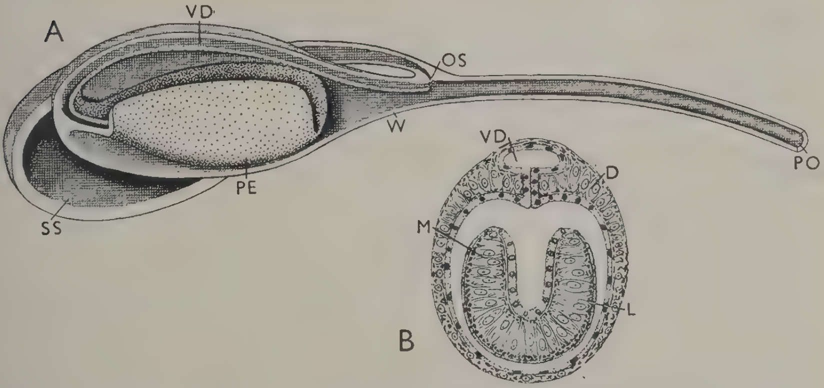

Fig. 2. *Turbonilla elegantissima.* A, Copulatory organs. The right wall of the sperm sac, the penial sheath, the vas deferens and of the posterior part of the penis has been removed. × 122. B, Transverse section through penis and its sheath. × 271. D, dilator muscles of penial sheath; L, longitudinal muscles of penis; M, muscles running between epithelia of penis; OS, opening of sperm sac into penial sheath; PE, penis; PO, opening of penial sheath beneath mentum; SS, sperm sac; VD, vas deferens; W, wall of penial sheath.

The penis is invaginable (Fig. 2A, PE), as in other pyramidellids, and when at rest lies in the haemocoel, retracted into a tubular sheath (W) with which its walls are confluent. The sheath is broad posteriorly where the retracted penis lies, and its narrow anterior end passes through the nerve ring to open beneath the mentum (PO). It is ventral to the introvert. A large muscular pouch, the sperm sac (SS), lined by a low columnar epithelium on which fine cilia are closely set, opens into the dorsal wall of the sheath, in front of the tip of the retracted penis. The opening is surrounded by a sphincter. The structure of the penis is unusual in that it contains neither blood spaces nor duct. When retracted into the sheath it has the appearance of a long muscular scoop attached posteriorly to the wall of the sheath. On to its concave surface, at the posterior end, opens the vas deferens, which is a deep longitudinal groove running along the dorsal wall of the sheath between the mouth of the sperm sac and the base of the penis. The lips of this groove (at least in fixed and dissected specimens) are firmly pressed together so that it may function as a duct. The vas deferens, the rest of the sheath and the penis are covered by cuticularized epithelium. The entire space between the upper and lower epithelia of the penis is occupied by three sets of intrinsic muscles: one series of fibres runs between the two epithelia (Fig. 2B, M); antagonizing these are bundles of longitudinal fibres under the lower epithelium (L); and, beneath the upper epithelium, on to which the vas deferens discharges, fibres run transversely from edge to edge with a few running longitudinally. It is assumed that, as in *Odostomia* spp., the sperm sac is filled with spermatozoa prior to copulation, for it is difficult to see how they could reach it when the penis is protruded. There is another sac, similar in histology and slightly smaller, which lies in the haemocoel above the anterior end of the retracted introvert and opens on to the propodium not far from the genital aperture. The opening is median to that of the pallial duct and posterior to it. There is no evidence as to the use of this pouch, since it has always appeared empty. Perhaps it is concerned with copulation and functions as a bursa, receiving the sperm from the penis and storing them temporarily, and expelling them later to the groove by which it is connected to the genital duct.

The penis in most gastropods is distended with blood at the time of copulation and at other times is relatively small. In *Omalogyra atomus* (Fretter, 1948) and *Turbonilla elegantissima*, both highly specialized species, the organ is unusual in that it contains neither blood spaces nor glands and the musculature is pronounced. The protrusion of the penis in *Turbonilla* is presumably brought about by pressure on the blood in the haemocoel aided by the muscles of the penial sheath.

The eggs of *T. elegantissima* are not known. Lebour (1936) describes and figures the young which even when very small (0·25 mm. across the shell) may be found with the adults in muddy and stony ground. She suggests that there is a very short free-swimming stage in the life history, and this would agree with what happens in species of *Odostomia*.

## SUMMARY

*Turbonilla elegantissima* is a pyramidellid, ectoparasitic on *Audouinia tentaculata* and *Amphitrite gracilis*, attaching to the tentacles, and sometimes to the gills of *Amphitrite*, by means of an oral sucker, piercing by a stylet—a modified jaw—and sucking its food by a buccal pump. It burrows in silt.

The alimentary canal varies from the structure in *Odostomia* and *Chrysallida* in details which are relatively unimportant and confined to its highly modified

anterior part. Thus the stylet, and consequently the oral tube, is very short, and in the tube there is only one channel for both stylet and food; the opening of the introvert is on the dorsal surface of the mentum, subterminally, and the surface of the introvert is not papillated; the buccal pump is short, arising behind the sucker, and has no caecum; the oesophagus is divisible into anterior and posterior sections, distinguished by their musculature and by the fact that the salivary ducts run within the longitudinal muscles of the anterior part.

In the reproductive system there is greater specialization than in *Odostomia* and *Chrysallida*: for the opening of the pallial hermaphrodite duct is on the propodium. The penis, scoop-shaped and concealed within a sheath, has neither blood spaces nor duct, and its musculature is pronounced. There is a muscular pouch in the haemocoel of the head, opening on the propodium close to the hermaphrodite genital aperture, which may be a bursa copulatrix.

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# THE BREEDING OF *CREPIDULA FORNICATA* (L.) IN THE RIVER BLACKWATER, ESSEX

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(Text-figs. 1–4)

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## INTRODUCTION

The chain-forming prosobranchiate gastropod *Crepidula fornicata* is not indigenous to British waters, but has been introduced during the last 70 or 80 years, probably from North America, upon imported oysters, and, during this period, has spread to most of the oyster beds on the south-east and south coasts of this country (see Orton, 1950*b*, for a recent discussion of its present distribution). In spite of the interest shown in this species because of its detrimental effect upon oyster culture, and because of its well-known change of sex from male to female, little is known in the literature of its breeding habits here, or in North America. Conklin (1897) states that the spawning period in New England lasts from early summer to about mid-August, no larvae being found in late August. Murie (1911), in discussing the introduction of this species, elaborates upon Conklin's observations, and gives evidence that females, in samples of *Crepidula* taken from the River Colne in May and September 1898, contained spawn beneath their shells. Orton (1912*a*, p. 438) states that he is 'informed by Professor Conklin that American Crepidulae begin to spawn in May and possibly in April, whilst English Crepidulae begin to spawn in early March'. In a footnote, he adds 'Crepidula spawned in tanks at Plymouth in early February'.

Later workers upon *Crepidula* have added little to our knowledge of the breeding period, although Coe (1936, 1938) has investigated the sex change in several species, in greater detail than Gould (1919). Orton (1909) has described the occurrence of protandric hermaphroditism in *C. fornicata* and (1912*b*) the method of feeding. Thorson (1946), whilst conducting extensive plankton investigations in Danish waters, recorded the early free-swimming stages of *C. fornicata* off north-west Jutland, in July 1940, but observed no later stages.

The author is indebted to Messrs Wombwell and French, of the Tollesbury and Mersea Native Oyster Co., for arranging the collection of regular samples of *Crepidula*. The author is also indebted to Emeritus Professor J. H. Orton, of Liverpool University, for generous advice and criticism, to his present colleague Dr D. J. Crisp for much useful advice, particularly upon statistical problems, and to the Directors of Imperial Chemical Industries Paints Division, under whose auspices the investigation was conducted.

## SUMMARY OF THE LIFE HISTORY OF *CREPIDULA FORNICATA*

The anatomy and histology of the reproductive system of *C. fornicata* are well known (Orton, 1909; Gould, 1917; Coe, 1936).

Briefly, the gonad consists of an irregular lobulated organ lying along the intestine and between the lobes of the digestive gland. In the functional males it is reddish brown in colour, whilst the female gonad is bright yellow. The diverticulae of the gonad give rise to the gonoduct anteriorly. The gonoduct in the functional male consists of a very convoluted seminal vesicle, which is continued as a narrow vas deferens to open upon a ciliated groove, which runs forward, on the right side of the animal, to a large grooved muscular penis, situated behind the base of the right tentacle.

On the completion of the functional male phase, the penis degenerates, cells being sloughed off from the brown tip (Gould, 1917). As the penis becomes smaller, the width of the gonoduct increases and the inner walls become folded longitudinally. The distal part of the gonoduct develops into a prominent uterus with folded walls, into which a number of seminal receptacles open.

Whilst these changes are taking place, the penis becomes greatly reduced, and is finally represented by a minute brown scar. The gonad, which even in the male phase contains small ova, develops rapidly as oogenesis takes place, becoming a bright yellow when fully functional. Coe (1938) found that the period of sexual transformation from male to female in isolated individuals was 61 days, but was considerably longer for males forming part of a 'chain'.

The eggs are laid in a bunch of stalked balloon-shaped capsules, united basally to a common stem, fastened to the substratum and, as in *Vermetus*, protected by the parent whilst development is in progress. The capsule has thin, cream-coloured walls, and contains *c.* 250 eggs, each 150–170 $\mu$ in diameter when initially spawned, floating in the intra-capsular fluid.

The embryonic development has been described in great detail by Conklin (1897). At the end of embryonic development, the larvae escape as advanced veligers through an apical split in the egg sac, to lead a free-swimming life until settlement occurs. The free-swimming veliger larvae possess shells 260 $\mu$ long, 190 $\mu$ broad and 170 $\mu$ high (mean of 100 measurements), with a two-third to three-quarter whorl.

In the adults, the functional male phase can be readily distinguished externally by the development of a coiled seminal vesicle, a long black penis, and a red brown gonad, whilst the functional female possesses a prominent uterus and a yellow gonad. Not infrequently a female is found with a small brown rudimentary penis. Orton (1909) gives diagrams of the functional male and female phases, with several intermediate stages.

## MATERIALS AND METHODS

The investigation of the breeding of *Crepidula fornicata* was commenced in May 1946, and was continued until December 1947. In 1946, samples of about 50 'chains' (i.e. *c.* 150 females) of *Crepidula* were obtained fortnightly from the oyster beds in Thirslet Creek, near Tollesbury (River Blackwater), Essex, although larger samples from Mersea Quarters (West Mersea) were examined when personal visits were made to the locality. No samples could be obtained from the River Blackwater during February and early March 1947, owing to the presence of extensive ice floes. From mid-March, however, until November, regular weekly samples of the same size (i.e. *c.* 50 chains) as employed in the previous year (1946), were obtained from Mersea Quarters (see Admiralty Charts 3740–3741). Except when personal collections were made, all samples were wrapped in damp sacking, packed in a wicker-work basket, and were dispatched by rail on the afternoon of the day of collection. They were usually received at Liverpool late the following morning, in good condition, even during the period of high temperatures during the summer of 1947. A few observations were made as opportunity arose at Burnham-on-Crouch in 1948, 1949 and 1950, but no systematic study was attempted.

The samples were examined for sex, gonad development, and presence of, and stage of development of the embryos. Shell lengths were usually recorded. Complete chains (i.e. those unbroken with the basal member present) only were employed.

The embryos were referred to seven categories, each corresponding to a readily distinguished stage in development as follows:

*Stage* 0. Comprising those females with well-developed ovaries, containing ripe ova, and which are ready to spawn.

*Stage* 1. 1- to 8-celled stage, usually an orange or deep yellow in colour (Fig. 1*a*).

*Stage* 2. 8-celled stage, to the end of gastrulation (Fig. 1*b*). The colour of the embryos in this stage is predominantly yellow but is sometimes cream. Owing to the amount of albuminous fluid contained within the egg cases, the embryos are normally difficult to separate for examination.

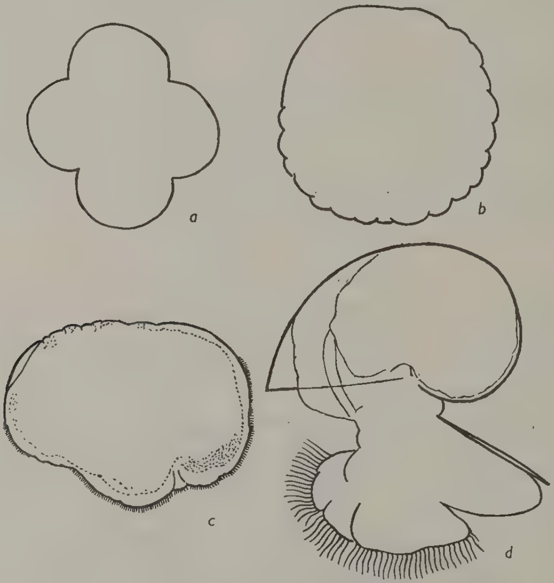

Fig. 1. *Crepidula fornicata.* Stages of embryonic development: *a*, Stage 1; *b*, Stage 2; *c*, Stage 3; *d*, Stage 5.

*Stage* 3. The 'pre-veliger' stage, in which gastrulation is complete, and the archenteron and stomodeum are well formed, the latter usually being prominent. The shell gland can usually be observed. The embryo is well ciliated (Fig. 1*c*). The colour is usually yellow to light yellow and the embryos are normally more readily separated than in the previous stage.

*Stage* 4. Early veliger stage, with well-developed velum, and shell, but with a less advanced internal organization than the next stage. The colour is usually a light yellow to yellow-brown. The embryos are readily separable in sea water.

*Stage* 5. Later veliger stage, ready to hatch (Fig. 1*d*). The shell is well formed, of a broad tumid appearance. The velum is slightly 4-lobed and very strongly ciliated. The margin of the velum is usually darkly pigmented. The foot is well developed and ciliated, with a dark pigment spot anteriorly. The gut is filled with granules, and is darkly pigmented. The embryos at this stage appear brown or dark grey to the naked eye.

*Stage* 6. Hatched stage, represented by empty egg capsules.

The stage of development of the embryos was determined microscopically, the criterion of colour alone not being sufficiently definite to ensure accurate classification into the appropriate category.

During both seasons, the percentage of females bearing embryos in Stage 1, except at the beginning of the period of spawning in 1947, was low, and followed the general course of spawning closely. It is possible that these embryos were the result of forced spawning, extrusion of the ova occurring during the process of dredging, and hauling the trawl. As 24 hr. normally elapsed before examination could be commenced, there was ample opportunity for early segmentation to occur. It is doubtful whether such premature spawning occurred in transit (unless the material was very roughly handled), as samples collected on the same ground at West Mersea, part of which were examined immediately, and part after 24 hr. storage in air, showed no significant difference in numbers of Stage 1 embryos, although many more advanced Stage 1 embryos were present after 24 hr. than immediately after collection. Also, unsegmented ova were never observed in the material examined at Liverpool, or 24 hr. after collection at West Mersea. However, the fact that most of these Stage 1 embryos were fertilized and actively segmenting suggests that the female *Crepidula* bearing them were ripe and ready to spawn.

*Sea temperatures, etc.* In order to investigate a possible correlation between sea temperature and the breeding of *Crepidula* records of the bottom temperature were made twice daily (early morning and early afternoon) in Thirslet Creek, near Tollesbury, from September 1946 until December 1947. From the end of February until December 1947 sea temperatures were also taken twice daily in Thornfleet (West Mersea) at 7 a.m. and 1 p.m. The daily means of the 1947 Thornfleet bottom temperatures are shown in Fig. 4. Standard sea-water thermometers (checked against an N.P.L. standard) with small buckets around the bulbs were employed in both localities. During 1947 the daily mean bottom temperatures in the two localities differed on no occasion by more than ±2·0° F.

No salinity or pH measurements were made.

## SPAWNING IN 1946 AND 1947 ON THE BLACKWATER OYSTER BEDS

The results of the observations upon the spawning of *C. fornicata* made in 1946 and 1947 are given in Tables I and II respectively. In Table I, the numbers of females bearing Stages 2 and 3, and 4 and 5 embryos are combined, but in Table II (for 1947) each category of embryonic development is given separately. The information obtained in the two years of study is shown graphically in Figs. 2 and 3 for 1946 and 1947 respectively. With the exception of the total

## TABLE I. *CREPIDULA FORNICATA*. SPAWNING AT TOLLESBURY (THIRSLET CREEK) AND WEST MERSEA (MERSEA QUARTERS) IN 1946

| | | | | No. of females with | | | | Cumulative percentage, i.e. percentage of females with spawn which has developed beyond | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Date, 1946 | Locality | No. of chains examined | No. of females | Spawn (total) | Stage 1 spawn | Stages 2 and 3 spawn | Stages 4 and 5 spawn | Stage 0 | Stage 1 | Stages 2 and 3 | Mean nos. of females per chain |
| 8. v. | Toll. | 44 | 136 | 110 | 22 | 42 | 46 | 80·9 | 64·7 | 33·8 | 3·10 |
| 17. v. | Toll. | 35 | 108 | 102 | 18 | 31 | 52 | 94·4 | 77·0 | 48·1 | 3·09 |
| 20. v. | W.M. | 100 | 298 | 276 | 15 | 88 | 173 | 92·7 | 87·6 | 58·0 | 2·98 |
| 29. v. | Toll. | 35 | 123 | 104 | 21 | 37 | 51 | 84·5 | 71·6 | 41·5 | 3·54 |
| 11. vi. | Toll. | 50 | 184 | 166 | 26 | 124 | 16 | 90·2 | 76·1 | 8·7 | 3·68 |
| 19. vi. | W.M. | 50 | 147 | 112 | 5 | 38 | 69 | 76·0 | 72·8 | 46·9 | 2·94 |
| 29. vi. | Toll. | 50 | 180 | 138 | 24 | 73 | 41 | 76·7 | 57·7 | 22·8 | 3·60 |
| 10. vii. | Toll. | 36 | 120 | 62 | 12 | 42 | 8 | 51·6 | 41·6 | 6·7 | 3·34 |
| 17. vii. | W.M. | 50 | 151 | 59 | 18 | 15 | 26 | 39·0 | 27·2 | 17·2 | 3·02 |
| 29. vii. | Toll. | 28 | 79 | 14 | 2 | 10 | 2 | 17·2 | 15·2 | 2·5 | 2·82 |
| 2. ix. | Toll. | 51 | 177 | 24 | 15 | 6 | 3 | 13·5 | 5·1 | 1·7 | 3·47 |
| 19. ix. | Toll. | 50 | 164 | 3 | 0 | 3 | 0 | 1·8 | 1·8 | 0 | 3·38 |
| 8. x. | Toll. | 30 | 97 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3·23 |
| 26. xi. | Toll. | 25 | 79 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3·16 |

Toll. = Tollesbury. W.M. = West Mersea.

## TABLE II. *CREPIDULA FORNICATA*. SPAWNING AT WEST MERSEA (MERSEA QUARTERS) IN 1947

| | | | Nos. of females bearing spawn | | | | | | | Cumulative percentage, i.e. percentage of females with spawn which has developed beyond | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date, 1947 | No. of chains examined | No. of females | Total | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 | Stage 6 | Stage 0 | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 | Mean nos. females per chain |
| 19. iii. | 40 | 105 | 0 | 0 | — | — | — | — | — | 0 | 0 | — | — | — | — | 2·62 |
| 17. iv. | 35 | 101 | 0 | 0 | — | — | — | — | — | 0 | 0 | — | — | — | — | 2·88 |
| 23. iv. | 40 | 92 | 25 | 25 | 0 | — | — | — | — | 27·0 | 0 | 0 | — | — | — | 2·30 |
| 29. iv. | 45 | 135 | 89 | 84 | 5 | 0 | — | — | — | 66·0 | 3·7 | 0 | — | — | — | 3·00 |
| 6. v. | 45 | 112 | 82 | 52 | 30 | 0 | — | — | — | 73·0 | 36·6 | 0 | — | — | — | 2·50 |
| 14. v. | 32 | 75 | 56 | 1 | 34 | 21 | 0 | 0 | 0 | 74·6 | 73·4 | 28·0 | 0 | 0 | 0 | 2·34 |
| 20. v. | 46 | 105 | 100 | 15 | 13 | 13 | 24 | 27 | 8 | 95·2 | 81·0 | 68·6 | 56·1 | 33·4 | 7·6 | 2·28 |
| 4. vi. | 56 | 121 | 115 | 7 | 16 | 21 | 28 | 22 | 21 | 95·0 | 90·1 | 76·0 | 58·7 | 35·5 | 17·3 | 2·16 |
| 16. vi. | 47 | 111 | 106 | 19 | 34 | 16 | 19 | 3 | 15 | 95·5 | 78·4 | 47·7 | 33·1 | 16·2 | 13·5 | 2·36 |
| 25. vi. | 44 | 78 | 67 | 1 | 19 | 9 | 4 | 4 | 30 | 85·9 | 84·6 | 60·3 | 48·7 | 43·6 | 38·5 | 1·66 |
| 2. vii. | 45 | 100 | 90 | 7 | 55 | 4 | 4 | 2 | 18 | 90·0 | 83·0 | 28·0 | 24·0 | 20·0 | 18·0 | 2·22 |
| 9. vii. | 46 | 104 | 80 | 0 | 30 | 9 | 19 | 10 | 12 | 77·0 | 77·0 | 48·1 | 39·4 | 12·1 | 11·5 | 2·26 |
| 17. vii. | 27 | 68 | 27 | 0 | 15 | 1 | 3 | 2 | 6 | 39·7 | 39·7 | 17·7 | 16·2 | 11·8 | 8·8 | 2·52 |
| 28. vii. | 45 | 128 | 56 | 0 | 26 | 0 | 9 | 6 | 15 | 43·7 | 43·7 | 23·4 | 23·4 | 16·4 | 11·7 | 2·84 |
| 12. viii. | 25 | 80 | 4 | 0 | 0 | 1 | 1 | 0 | 2 | 5·0 | 5·0 | 5·0 | 3·7 | 2·5 | 2·5 | 3·20 |
| 20. viii. | 25 | 69 | 4 | 0 | 1 | 1 | 2 | 0 | 0 | 5·8 | 5·8 | 4·3 | 2·9 | 0 | 0 | 2·76 |
| 3. ix. | 37 | 119 | 19 | 0 | 8 | 3 | 6 | 1 | 1 | 16·0 | 16·0 | 9·2 | 6·7 | 1·6 | 0·8 | 3·22 |
| 18. ix. | 44 | 153 | 7 | 0 | 0 | 0 | 0 | 0 | 7 | 4·6 | 4·6 | 4·6 | 4·6 | 4·6 | 4·6 | 3·48 |
| 7. x. | 26 | 86 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3·30 |

percentage of females spawned in each sample, the results are given as cumulative percentages, i.e. in each sample the proportion of females carrying spawn which has developed beyond each category is plotted as a percentage of the total females present in the sample. This type of cumulative frequency distribution, because of the grouping of results, enables the temporal relationships in such biological behaviour as spawning and development to be presented more clearly. The method is similar to that employed in survival investigations in insecticide studies.

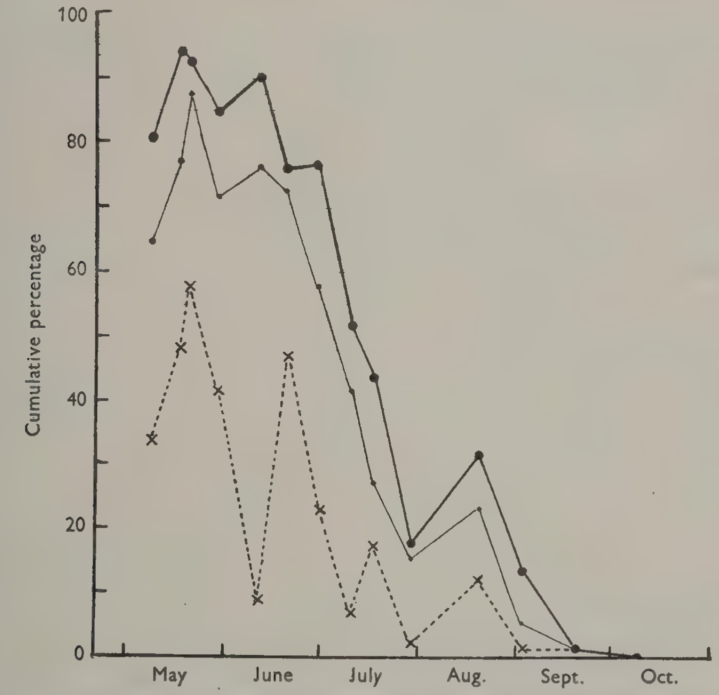

Fig. 2. *Crepidula fornicata.* Spawning behaviour at Tollesbury (Thirslet Creek) in 1946. Percentage of females bearing spawn developed beyond: ●———●, Stage 0; ·———·, Stage 1; ×– – – –×, Stage 3.

### *Significance of Results*

The samples of *C. fornicata* employed in this investigation can be considered random, as (i) they were not chosen for any particular attribute, other than that the chains should be complete, i.e. broken chains were rejected, and (ii) each sample was made up of chains taken from several hauls upon the same bed.

In order that the significance of the differences between successive samples might be assessed, the data obtained from the examination of the samples were treated statistically (Table III).

In column 6 of Table III the standard error of the percentage of females bearing spawn which has developed beyond Stage 2 (i.e. the sum of all females with embryos of the pre-veliger and later stages) for each sample in 1947 is given. By taking this stage of development for statistical treatment, the inclusion of possibly prematurely spawned females is avoided.

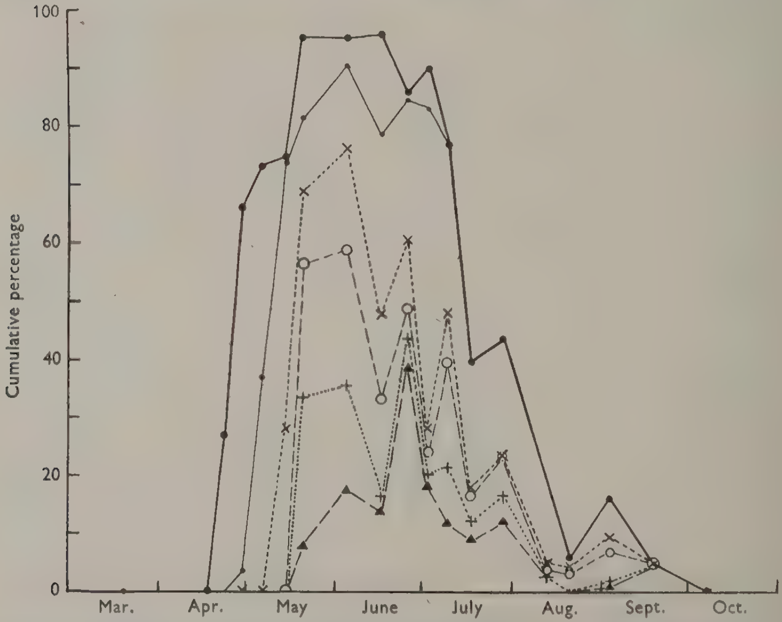

Fig. 3. *Crepidula fornicata.* Spawning behaviour at West Mersea (Mersea Quarters) in 1947. Percentage of females bearing spawn developed beyond: ●———●, Stage 0; ·———·, Stage 1; ×– – – –×, Stage 2; o– – – –o, Stage 3; +- - - -+, Stage 4; ▲———▲, Stage 5.

In column 7 are given the values of $\chi^2$ and the corresponding probability calculated from the actual numbers of females with spawn developed beyond Stage 2 in successive pairs of samples, employing the 2 × 2 Contingency Table method. No allowance has been made in this treatment for the association of females in chains, and the assessment of significance of the differences between pairs of samples is the most favourable obtainable, i.e. the assumption is that the females were sampled at random. As only complete chains were sampled at random, a stricter analysis, representing the most unfavourable condition, in which the numbers of females in each sample were reduced in proportion to the number of chains in the sample, was employed, and the significance assessed by the method for small samples drawn from a Binomial Distribution. The values for $\chi^2$ thus obtained are given in column 8 of Table III.

The differences which are significant upon a basis of $P=0{\cdot}05$ are underlined in columns 7 and 8 of Table III. Use will be made of these significant differencesi n the discussion upon possible periodicity in spawning (see p. 59).

### *Length of Breeding Period*

The first sample of *Crepidula* examined in 1946 (8 May) was obtained after the breeding period had commenced, about two-thirds of the females bearing spawn and of which a half contained veliger larvae. Spawning had thus begun some time previously. Subsequently, egg capsules, containing embryos in various stages of development, were present in all samples until mid-September (see Fig. 1), after which date none was seen until the following season.

TABLE III. *CREPIDULA FORNICATA*. SIGNIFICANCE OF SPAWNING RESULTS, 1947

| (1) Date 1947 | (2) No. of chains examined | (3) No. of females | (4) No. of females with spawn passed through Stage 2 | (5) Percentage of females with spawn which has passed through Stage 2 | (6) Percentage standard error of females in '5' (Binomial) + or − | (7) 2 × 2 contingency table | | (8) Binomial sampling on basis of no. of chains | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | $\chi^2$ | approx. $P$ | $\chi^2$ | approx. $P$ |
| 23. iv. | 40 | 92 | 0 | — | — | — | — | — | — |
| 29. iv. | 45 | 135 | 0 | — | — | — | — | — | — |
| 6. v. | 45 | 112 | 0 | 0 | 0 | | | | |
| 14. v. | 32 | 75 | 21 | 28·0 | 7·9 | **29·3** | <0·001 | **9·6** | 0·003 |
| 20. v. | 46 | 105 | 72 | 68·6 | 6·9 | **29·6** | <0·001 | **13·1** | <0·001 |
| 4. vi. | 56 | 121 | 92 | 76·0 | 5·7 | 1·42 | 0·14 | 3·05 | 0·69 |
| 16. vi. | 47 | 111 | 53 | 47·7 | 7·3 | **18·0** | <0·001 | **8·9** | 0·004 |
| 25. vi. | 44 | 78 | 47 | 60·3 | 7·4 | 3·15 | 0·08 | 0·44 | 0·52 |
| 2. vii | 45 | 100 | 28 | 28·0 | 6·7 | **18·3** | <0·001 | **6·10** | 0·014 |
| 9. vii. | 46 | 104 | 50 | 48·1 | 7·4 | **8·30** | 0·006 | 2·80 | 0·09 |
| 17. vii. | 27 | 68 | 12 | 17·7 | 7·4 | **16·9** | <0·001 | **13·1** | <0·001 |
| 28. vii. | 45 | 128 | 30 | 23·4 | 6·3 | 0·89 | 0·36 | 2·60 | 0·11 |
| 12. viii. | 25 | 80 | 4 | 5·0 | 4·4 | **12·1** | <0·001 | **9·1** | 0·003 |
| 20. viii. | 25 | 69 | 4 | 4·3 | 3·9 | 0·04 | 0·84 | 0·00 | 1·00 |
| 3. ix. | 37 | 119 | 11 | 9·2 | 4·7 | 1·34 | 0·25 | 1·04 | 0·29 |
| 18. ix. | 44 | 153 | 7 | 4·6 | 3·3 | 2·16 | 0·15 | 0·21 | 0·66 |
| 7. x. | 26 | 86 | 0 | 0 | — | — | — | — | — |

$\chi^2 g = 1 (P=0{\cdot}05) = 3{\cdot}841$.

Values of $\chi^2$ in heavy type indicate those significant on the $p=0{\cdot}05$ criterion.

In 1947 the first females bearing spawn were observed on 23 April, initial spawning having thus occurred between 17 and 23 April. All the embryos were, however, in Stage 1, and may thus have been spawned prematurely. The first females with Stage 2 embryos were observed on 29 April. From this time developing embryos were present until mid-September (18th) when empty egg cases only were observed. At Burnham-on-Crouch in 1948 and 1949, female *Crepidula* with developing embryos were observed from April until September.

Thus, on the Essex oyster beds, spawning of *Crepidula* would appear to commence in early spring, and to continue until September in most years, giving a breeding period of about 5½ months' duration. The breeding period on the Essex oyster beds is therefore rather longer than that for the same species upon the New England beds as described by Conklin (1897). Orton's (1912*a*) observation that *C. fornicata* in English waters begins to spawn in March was not borne out by the 1947 observations, but, in that year, water temperatures in the Blackwater were very low (30° F. at the beginning of the month, rising to 42° F. at the end), following the abnormal weather in February, when ice was present on many parts of the east coast. In 1948, a single sample from Tollesbury (Thirslet Creek), taken on 6 April, showed that spawning had commenced a few days previously, whilst *Crepidula* began to spawn at Burnham-on-Crouch in 1950 immediately before 30 March. It would thus seem that *Crepidula*, in a warm spring, spawns on the Blackwater oyster beds at least in late March or early April. This view is supported by Prof. J. H. Orton who, in a personal communication, states that there is little doubt that spawning commences in a normal spring in March.

### *Sea Temperature and the Commencement of Spawning.*

In 1946, no observations of the onset of spawning in *Crepidula* in relation to sea temperature could be made. In 1947, however, the onset of spawning was carefully followed. Initial spawning (possibly premature) took place between 17 and 23 April, whilst the first Stage 2 embryos were found in the sample collected on 29 April. During this period the mean daily sea temperature remained at a little above 50° F. until about 24 April, having risen from 45° F. to this value between 12 and 17 April, and rose to 52° F. between 24 and 30 April. Thus spawning commenced at a period when the sea temperature had risen slightly above 50° F.

No systematic observations were possible in following years, but the sea temperature at Tollesbury (Thirslet Creek) rose above 50° F. at the end of March 1948, and, as has been stated previously, a sample of *Crepidula* obtained on 6 April of that year supplied data suggesting that spawning had commenced a few days previously. No observations were made in 1949, but in 1950 spawning commenced at Burnham-on-Crouch at the end of March, when the sea temperature had risen to *c.* 51° F. It is therefore possible that *Crepidula* does not spawn until the sea temperature rises to, or above, 50° F.

### *Temperature and Duration of Spawning Period*

Although in 1947 at West Mersea initial spawning took place shortly after the sea temperature rose above 50° F., spawning ceased a considerable time before the occurrence of the autumnal homothermal epoch, the ovaries of the female *Crepidula* showing exhaustion during July. Thus, in *Crepidula* from the Blackwater beds, as in *Ostrea* (Korringa, 1947), temperature does not appear to determine the duration of the breeding period directly, and it would seem that the length of the breeding period is determined, rather, by the rate of exhaustion of the gonads, and the rate of regeneration of ova and sperm. Spawning in *Crepidula* does not appear to be limited by the high maximum temperatures attained during the summer, but there is some evidence that the higher summer temperatures in the Blackwater in 1947 caused a more rapid spawning, and consequently an increased rate of exhaustion of the gonads, than in 1946.

### *Periodicity in Spawning*

The results obtained in 1946, owing to rather infrequent sampling, do not provide definite evidence of periodic spawning, in the sense that a proportion of females in the population tend to release their ova in concert several times during the breeding period. Two well-defined maxima in the proportion of females bearing spawn of Stages 4 and 5 (i.e. veligers) occurred in the samples from West Mersea collected on 20 May and 19 June (See Table I and Fig. 2), whilst two smaller ones were recorded on 17 July and 19 August, although these are probably not significant statistically. On the latter date, however, a distinct maximum in early stages occurred. It would thus seem that, from the beginning of May until the end of the spawning period in September, three concerted spawnings took place, one before 20 May, one immediately before 11 June (before a new moon, or during the last quarter phase) and a final one, rather distinct from the main spawning period, immediately before 19 August (at or after a new moon).

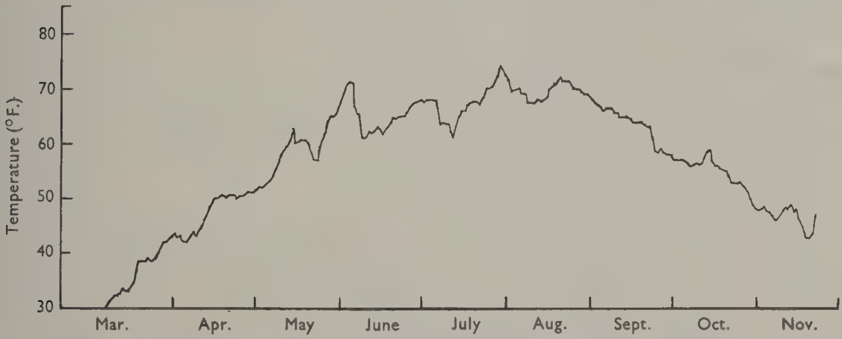

Fig. 4. Bottom temperatures at West Mersea (Thornfleet Creek) in 1947.

The greater frequency of sampling adopted in 1947 provides more definite evidence of concerted spawning (see Fig. 3). In this year, the first true spawning probably occurred immediately before 29 April, the first Stage 2 embryos being observed in a sample collected on this date (Table II). As the sea temperature had risen to and just above 50° some 10 days before (Fig. 4) it is unlikely that the temperature rise in itself acted as a spawning stimulus. This first spawning occurred contemporaneously with a first quarter lunar period. Spawning continued, and on 14 May, all embryos found, except in 1·3 % of the females, were in Stage 2 or Stage 3 of development, to be followed in the next sample on 20 May with a maximum of females bearing veliger larvae (Stages 4 and 5).

No evidence of a further concerted spawning was obtained until 16 June, when an increase in the proportion of females bearing Stages 1 and 2 embryos was recorded, followed in the next sample (25 June) by a significant peak in females with embryos developed beyond Stage 3, although the peak for females with embryos later than Stage 2 is not quite significant on the 5 % level ($P = 0{\cdot}08$) (see Table III). This spawning took place at a time when the sea temperature was *c.* 62° F., during a slight rise, after a rapid fall from 70° F. at the beginning of June (see Fig. 4), and also when the moon was waning (new moon, 18 June).

Spawning continued over the new-moon period, a maximum of Stage 2 embryos occurring in the next sample (2 July) to be followed by a significant maximum in older embryos 7 days later. This spawning, which included *c.* 7 % of females with Stage 1 embryos, took place when the sea temperature was *c.* 68° F., immediately before a full moon (3 July).

No further evidence of concerted spawning was recorded until the end of August, when the sea temperature was declining below 70° F., and the moon was waxing from first quarter to full. This spawning is possibly significant, although $P = 0{\cdot}15$ (Table III).

These observations are summarized in Table IV.

TABLE IV. POSSIBLE PERIODIC SPAWNING OF *CREPIDULA FORNICATA* AT WEST MERSEA, 1947

| Approx. date of spawning | Moon's phase | Sea temp. at spawning maximum (° F.) | Remarks |
|---|---|---|---|
| Between 17 and 23 April | New moon, 21 April | 50 | Probably premature spawning |
| Between 23 and 29 April | New moon, 21 April | 51·5 | First true spawning |
| Immediately before 16 June | New moon, 18 June | 62 | Max. in Stage 2 embryos followed 25 June by significant peak in Stage 4 and older embryos |
| Immediately before 2 July | Full moon, 3 July | 68 | Max. in Stage 2 embryos followed 9 July by significant peak in Stage 3 and older embryos |
| Between 17 and 28 July (approx. 25th) | New moon, 18 July | 67·5 | Not significant |
| About 25 August | Full moon, 31 August | 68 | Final spawning |

Although there is no definite indication of cyclic periodicity in spawning, the results obtained in 1947 show a marked tendency for a proportion of female *Crepidula* to spawn in concert, in a manner unassociated with temperature, or temperature fluctuations. Spawning, however, is evidently not limited to these periods for the mimima of the incidence of females with Stage 2 (i.e. young embryos) do not touch the zero ordinate until the end of the observed breeding period.

Of the four definite spawnings, two (first and last) occurred during a first-quarter lunar period, one immediately before or at the new moon, and one just before or at the full moon. Thus, three of the four concerted spawnings can be fitted into a first-quarter lunar period, and one to a last-quarter period. Similarly, three spawnings (all except the first) occurred at times when the tidal range was increasing, whilst, although the first spawning probably took place at a period of neap tides, the intensity of spawning greatly increased as the tidal range became greater (see Fig. 3). Unfortunately, the sampling frequency was too low to provide definite evidence for or against spawning towards the end of the lunar quarter periods when the tidal range and tidal currents would increase daily. The date of commencement of spawning at Burnham-on-Crouch in 1950 (29–30 March) lends some weight to this view, as spawning commenced from 1–2 days after the occurrence of the bottom of neap tides, i.e. when the tidal range was increasing.

Lunar periodicity in spawning has been fully discussed in the past by Fox (1924), Orton (1926, 1936), Amirthalingam (1928), Battle (1930, 1932), Wheeler & Brown (1936), Korringa (1947) and others. These writers have quoted many instances of spawning of marine invertebrates at spring tides, but there are few records of spawning at neap tides or at periods when the tidal range is increasing from the minimum at neaps, although Orton (1936) states that in 1927 there was a distinct tendency for *Ostrea edulis* from the Fal and Blackwater beds to spawn upon the neap tides preceding full moon tides. Some evidence of the spawning of *Pomatoceros triqueter* during periods of neap tides at Cullercoats was obtained in 1947 (Chipperfield, 1948).

The specific inducements which cause spawning in relation to lunar phases are obscure. Briefly, the factors which may be responsible are probably either (*a*) nutritional or (*b*) concerned with intrinsic rhythms.

There has been little investigation into the possibility that cyclic changes in nutrition related to the lunar and tidal periods induce spawning, although Loosanoff & Nomezko (1946) have found that feeding of *Ostrea virginica* shows no relationship to tidal ranges or periods of light and darkness. It seems possible that hitherto unknown factors such as the 'external metabolites' of Lucas (1947) may have an important bearing on these problems. Further, in some organisms, the rhythm of spawning appears to be intrinsic, e.g. in *Convoluta* the spawning of eggs takes place during the neap tides even *in vitro*.

There is little evidence that moonlight, or its absence, or the greater illumination of the sublittoral zone at the occurrence of low water during the hours of daylight, has any effect on immersed animals as a spawning inducement (Amirthalingam, 1928). Amongst the hydrographical effects of tides are the effect of alternating hydrostatic pressures, the greatest range being produced at spring tides; the variation in water temperature due to the more rapid warming and cooling of the intertidal zone at low water; and the variations in the magnitude of the tidal currents flowing at springs and neaps. Amirthalingam (1928) feels there is little evidence that hydrostatic pressure influences spawning in *Aequipecten*, whilst Orton (1936) suggests that a decrease in hydrostatic pressure with an increase in temperature may be responsible for initiating spawning in *Ostrea* on spring tides. Korringa (1947) also favours the effect of rhythmic variations in hydrostatic pressure as spawning inducements, whilst Battle (1932) suggests that the increase in pressure at spring tides causes spawning in *Yoldia sapotilla*. The presence of pressure-sensitive organs has not, as yet, been demonstrated in marine invertebrates. Variations in the velocity of tidal currents at springs and neaps may influence spawning, either directly or indirectly, e.g. via nutritional channels.

No precise spawning stimulus or series of factors contributing to the spawning stimulus in *Crepidula* can be elicited from the observations made in 1947. Spawning in *Crepidula* appears to be independent of temperature once a value of 50° F. has been attained. Tidal currents run swiftly both in the Blackwater and the Crouch, whilst the difference between the tidal range at springs and neaps is fairly large (about 5 ft. mean). Thus either of these factors may be responsible for the tendency towards concerted spawning of *Crepidula* in 1947.

### *Duration of Embryonic Life*

Owing to the low sampling frequency adopted in 1946, and the commencement of observations when the spawning period was well advanced, no reliable estimate of the duration of embryonic life of *Crepidula* can be made from the data. The data obtained from the more frequent observations in 1947, however, can be utilized for this purpose.

If it is assumed that the first normal true spawning occurred between 23 and 29 April, the first female *Crepidula* bearing Stage 3 embryos (pre-veligers) were observed in the sample taken on 14 May (28%), and the first fully developed veligers (Stages 4 and 5), and the first empty egg capsules on 20 May. Of the Stage 3 embryos observed on 14 May, a number were very advanced, and, if these may be considered as the first spawned embryos, they may be represented in the sample of 20 May by the recently emptied egg capsules. Similarly, the bulk of the veliger spawn (Stages 4 and 5) in the sample of 20 May probably represent those embryos which were spawned between 29 April and 6 May. These relationships are clearly illustrated in Fig. 2.

Thus, at the beginning of the spawning period, when sea temperatures range between 50 and 55° F., the first pre-veligers appear about 14 days after spawning, and the first true veligers in 14–21 days, whilst hatching occurs in

21–28 days. This estimate of the period of incubation is of the same order as Orton's (1912*a*) estimate that the eggs are 'protected by the mother *Crepidula* for about a month'.

The sequence of embryonic stages is less obvious later in the season, but it is possible that the spawning which occurred on about 18 June (see Table II) is represented in the sample of 28 June by the maximum of recently emptied egg capsules, whilst the peak in early veligers in the sample taken on 9 July represents those eggs spawned immediately before 2 July (see Fig. 2). Thus, during the period of higher water temperatures, development to the early veliger stage apparently takes place in about 7 days, and the hatching stage in about 10–14 days.

Thus, at the beginning of the spawning period, embryonic development in *Crepidula* would appear to take about twice as long as in June and July. The shorter duration of the veliger stages, particularly Stage 5, as compared with the younger stages, would explain the low incidence of females bearing Stages 4 and 5 embryos in the periodic samples.

### *Intensity of Spawning in* 1946 *and* 1947

The proportion of female *Crepidula* from the Blackwater bearing developing embryos and hatched egg cases (i.e. the total proportion spawned in each sample) in the 2 years are plotted in Figs. 1 and 2 for 1946 and 1947 respectively.

Even if allowances are made for the lower frequency of sampling in 1946, the gross spawning curves for 1946 and 1947 are very similar. In both years the maximum proportion of females bearing developing embryos or empty egg cases was *c.* 95%, or if those bearing Stage 1 (i.e. possibly premature) embryos are excluded as forced spawners, both maxima are reduced to about 90%. In both years these maxima were attained in May and were maintained during early June, the proportion of spawn-bearing females decreasing rapidly in July, the zero ordinate being approached in 1947 in mid-August. In both years a further spawning occurred at the end of the principal period, in August, and was rather earlier and almost twice as heavy in 1946 as in 1947 (*c.* 30% females with spawn in 1946, and 15% in 1947).

The females bearing embryos in Stages 4 and 5 (i.e. veligers) in one sample are unlikely to be represented by others in the next sample with embryos of the same stage of development, particularly during June and July, when embryonic development has been shown to be more rapid than at the beginning of the spawning period. Now, the aggregate percentage of females bearing Stages 4 and 5 embryos (i.e. veligers) in all samples from Tollesbury in 1946 is 179, or 230 if all samples from West Mersea are included except the one collected on 20 May (see Table I) only 3 days after a collection at Tollesbury, and in which, if spawning occurs more or less simultaneously throughout the Blackwater, veliger embryos arising from ova spawned at the same time are represented. The corresponding aggregate proportion for 1947 is 183%.

In view of the rapid development of the veliger embryos the aggregates given above would suggest the probability that the majority of the fully functional females of *Crepidula* spawn at least twice in a season. Further, the fact of periodic concerted spawning would suggest multiple spawning by some females at least, particularly as exhaustion of the ovaries was not of common occurrence until July, i.e. towards the end of the main spawning period.

### *Sequence of Spawning in the Chain*

The spawning of female *Crepidula* in 1947, during the initial spawning period, was analysed to show the percentage without spawn with Stages 2 and 3, and Stages 4 and 5 spawn and with empty capsules in each of the first two or three positions in the chains. (Note: the first individual in the chain is taken to be the basal member which adheres to the substratum, and which is designated the 'A' position. The next individual occupies the second or 'B' position and so on.) The proportion of chains with more than three functional females (i.e. fully developed ovary, well-developed uterus and with either a very rudimentary penis or none at all) is small, and has not been considered.

Out of a total of sixty-nine chains with two females, the basal member possessed more advanced embryos in thirty-one cases, the second member bore older embryos in twenty-three cases, and in the remaining fifteen examples, both the first and the second female members of the chain possessed embryos of the same stage of development.

Only twenty-eight chains possessing three females occurred in the samples of *Crepidula* taken during the early part of the breeding season. Of these twenty-eight chains, in eleven the basal females (i.e. the female in the 'A' position) possessed more advanced embryos, in nine those in the second or 'B' position, and in three only those in the third or 'C' position. Of the remaining chains, in one the females in the 'A' and 'B' positions bore embryos in the same stage of development, and in two those in positions 'B' and 'C' did so. The number of chains with four females was too small to allow any useful analysis to be made.

The numbers involved are not very large, and the statistical error is consequently high, but in the initial spawning period, females occupying the basal or first position appear to bear somewhat more advanced embryos than those in the second position, and that these, in turn, are somewhat more advanced than in the third position. Thus, there seems to be a very slight tendency in all chains for the basal and therefore oldest female to spawn first, with the next following closely. Females in the third position appear to spawn later than those in the first two (i.e. proximal) positions, this being especially noticeable towards the end of the spawning period. It is not known whether this is due to earlier copulation, which, in any case, occurs early in the year (Orton, 1912*a*). It is possible that the proximity of one or more males may delay the onset of maturity of the distal females, or that these spawn later, because they are younger females, maturing later normally.

*The Final Spawning.* In both 1946 and 1947, a small spawning occurred in August and September, as previously stated. The significance of this is rather obscure, for this spawning does not appear to be a further 'peak' of spawning in the main period, but one taking place after the termination of the latter. In view of Coe's (1938) work upon the sex change in *C. fornicata* from American beds, there is a possibility that the final spawning observed in 1946 and 1947 was due to the ripening of individuals which had changed their sex to become functional females during the summer. On the other hand, it is more likely that this final spawning took place in females which had spawned out earlier in the season, and which had, during the intervening period, re-developed ovaries sufficiently well to allow a further emission of ova to occur, whilst environmental conditions were still favourable to continued spawning.

TABLE V. *CREPIDULA FORNICATA*. POSITION IN CHAIN AND FINAL SPAWNING, 1947

| Position in chain (see p. 64) | Total no. examined | Stage of embryonic development | | | | |
|---|---|---|---|---|---|---|
| | | Stage 2 | Stage 3 | Stages 4 and 5 | Stage 6 | Total |
| (*a*) 20. viii. 47: | | | | | | |
| C | 25 | 0 | 0 | 0 | 0 | 0 |
| B | 25 | 1 | 1 | 1 | 0 | 3 |
| A | 13 | 0 | 1 | 1 | 0 | 2 |
| | 63 | 1 | 2 | 2 | 0 | 5 |
| (*b*) 3. ix. 47: | | | | | | |
| C | 37 | 0 | 1 | 5 | 0 | 6 |
| B | 37 | 4 | 0 | 0 | 1 | 5 |
| A | 28 | 4 | 2 | 2 | 0 | 8 |
| | 102 | 8 | 3 | 7 | 1 | 19 |

If the final burst of embryos were due to the spawning of those individuals which had changed their sex during the earlier part of the season, then the presence of embryos should tend to be confined to the distal females in the chain, i.e. to those females immediately adjacent to the males.

In Table V the distribution of females bearing embryos in two samples taken in 1947 during the final spawning period is analysed.

Thus, from the table, although it is possible that some of the distal females which had spawned were those which had changed their sex during the season, there is no evidence that the final spawning is confined to any particular position in the chain, and the figures would indicate that the final spawning is a question of adequate re-development of the ovaries whilst conditions for spawning are favourable.

## *Incidence of Females with a Rudimentary Penis*

During both 1946 and 1947, a number of females, with a well-developed uterus, and a yellow gonad filled with abundant oocytes but with a rudimentary (degenerating) penis, often 3–4 mm. in length, were a constant feature of the samples. These were invariably[1] the most distally situated females (i.e. those nearest the males), and obviously the youngest in the chain, having been the last to change from male to female.

The incidence of these females in samples examined 1947 from West Mersea between 29 April and 28 July is analysed in Table VI.

TABLE VI. *CREPIDULA FORNICATA*, 1947. INCIDENCE OF FEMALES WITH A RUDIMENTARY PENIS

| Date, 1947 | Total females in sample | Females with rudimentary penis | | | |
|---|---|---|---|---|---|
| | | (*a*) Total | (*b*) Without spawn | (*c*) With spawn | (*d*) Percentage of total females |
| 29. iv. | 135 | 9 | 8 | 1 | 6·7 |
| 6. v. | 112 | 9 | 9 | 0 | 8·0 |
| 14. v. | 75 | 5 | 5 | 0 | 6·7 |
| 20. v. | 105 | 1 | 0 | 1 | 0·9 |
| 4. vi. | 121 | 3 | 3 | 0 | 2·5 |
| 16. vi. | 111 | 3 | 3 | 0 | 2·7 |
| 25. vi. | 78 | 1 | 1 | 0 | 1·3 |
| 2. vii. | 100 | 7 | 4 | 3 | 7·0 |
| 9. vii. | 104 | 3 | 3 | 0 | 2·4 |
| 17. vii. | 68 | 7 | 7 | 0 | 10·3 |
| 28. vii. | 128 | 2 | 2 | 0 | 1·6 |
| Total | 1137 | 50 | 45<br>(4·0%) | 5<br>(0·4%) | —<br>(4·4%) |

It is apparent that the mean incidence of females with a rudimentary penis is low, although it is possible that more are present at the beginning and at the end of the main spawning period than during the period of most intense spawning. The low occurrence of females with a rudimentary penis bearing spawn is very significant, and would suggest that the bulk of such females are immature, in short chains at least.

## *Number of Female* Crepidula *in a Chain*

In Tables I and II, the mean number of females per chain in each sample is recorded in the final column.

Cursory examination of these figures suggests that, in 1946, the chains collected from Thirslet Creek (Tollesbury) contain rather more females than those collected from Mersea Quarters (West Mersea), i.e. a position nearer the open sea, whilst in 1947 rather more females occurred in those chains from Mersea Quarters collected during the latter part, and after the end, of the breeding period than during the early part.

These conclusions can be subjected to a strict test, employing the method based upon the distribution of '*t*'.

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[1] I am informed by Prof. Orton that this is not always applicable to long chains of *Crepidula*.

From the 1946 observations, the mean number of females in the chains from West Mersea is 2·98 (three samples), and, in chains from Tollesbury, 3·31 (eleven samples). Comparison of these samples, on the null hypothesis that they were drawn from the same population, gives a value for '$t$' of 2·14. As, from the tables (Fisher & Yates, 1948, p. 32) '$t$' for $P=0·05$ for 12 degrees of freedom is 2·18, it can be concluded that the probability of the Tollesbury *Crepidula* samples possessing more females per chain than the West Mersea *Crepidula* in 1946 is high, the difference between the sample means being significant on the $P=0·06$ level. A heavier settlement of spat, owing to the more restricted size and rate of flow of the water mass, or a lower mortality in Thirslet Creek may provide possible explanations.

In 1947 figures were similarly treated, the mean of the number of females per chain from 23 April to 17 July being compared with the mean for the period 28 July to 7 October. The sample taken on 25 June was omitted, as a large proportion of the longer chains were broken. The mean number of females per chain is 2·34 (ten samples) for the earlier period, and 3·13 (six samples) for the later period. From the comparison of these means by the normal methods a value for '$t$' of 5·34 was obtained. From the tables the values of '$t$' for 14 degrees of freedom for $P=0·05$ and $P=0·001$ are 2·145 and 4·140 respectively. Thus, the difference between the means is highly significant, and it would seem that, in 1947, the mean number of females per chain of *Crepidula* increased at the end of the spawning period owing, possibly, to a lower mortality at the end of the season compared with the period when spawning was intensive, or to a real increase in the number of females by the change of sex from male to female. As there was little evidence in the 1947 samples of a higher mortality during the spawning period, it is probable that the sex change is responsible for the increase in the number of females per chain.

## SETTLEMENT IN 1946 AND 1947 IN THE BLACKWATER

During the summer and early autumn of 1946, samples of culch and of adult *Crepidula* were examined carefully for the presence of *Crepidula* spat, but very few indeed were found, in spite of the high intensity of spawning, and the fact that abundant veligers were seen in plankton collected at West Mersea on 20 June.

In 1947, however, settlement was heavy. On 28 June, Mr French, who collected the samples at West Mersea, reported the presence of a few spat on the oyster culch, whilst a few minute *Crepidula* were taken from shells collected at Tollesbury on the 25th. By 2 July, spat was thickly clustered on old shells, particularly on the inner surfaces of dead *Crepidula* shells, and on the sheltered areas of oyster shells and culch. Few were found upon exposed surfaces of the shells and upon living *Crepidula* in the samples. A week later very large numbers of spat were present, and settlement continued until mid-August, thereafter declining rapidly. A small settlement, indicated by the presence of minute spat, took place in September, at a time when spat which had settled earlier were growing rapidly. Orton (1950*a*) has recently discussed the variations in the spatfall of *Crepidula* on the Essex oyster beds in 1945–1947.

### *Duration of larval life in* Crepidula.

Estimates of the duration of planktonic larval life based upon observations of release of larvae from, or the spawning of, the adults of sessile marine invertebrates, and of the initial settlement of spat upon appropriate substrata are notoriously inaccurate, depending, as they do, upon the assumption that the stock of larvae settling is the same as the stock which was spawned previously. Examples are well known in which, after a normal spawning, larvae developed beyond a certain stage are not seen in the plankton for a considerable period, e.g. *Verruca*. Thus, all estimates of larval life derived in this way must be interpreted with care.

Such an estimate for the duration of planktonic larval life in *Crepidula* can be obtained from the data obtained in 1947 for the Blackwater. The first hatched egg cases appeared in the sample taken on 20 May, whilst the first settled spat were observed at the end of June, thus giving a possible larval life of about 35 days.

## GROWTH OF SPAT

When a length of 3–5 mm. is reached, the young *Crepidula* become highly motile and migrate from their sheltered positions under shells, etc. and settle upon existing chains, usually taking up a terminal position, or one upon the side of an adult female. A few small individuals occasionally form short chains of two or three members. It is not known whether these chains of spat are permanent or whether the basal member can migrate, carrying the remainder of the chain. Few solitary *Crepidula* over 6 mm. in length were found on culch from the Essex oyster beds in 1947.

During this period of migration, and when permanent positions are taken up on existing chains, mortality is apparently high, for the number of small individuals (*c*. 6–12 mm.) observed on chains during the autumn is only a very small fraction of the total settlement on culch, etc., in the summer.

On 29 April 1947 some fifty smallest individuals from the chains in the sample were removed and measured. The range was from 7 to 26 mm. with a mean of 18 mm., which probably represents a fair growth of the previous season's spat and is in accordance with the observations of Orton (1914). Coe (1942) states that the growth rate on New England coasts is such that, at 1 year of age, *C. fornicata* are 18–28 mm. in length. Gould (1917), on the other hand, states that *C. fornicata* grew to 10–15 mm. in 2 months at Woods Hole. Such high growth rates do not appear to be attained amongst normal populations in the Blackwater, but no accurate information is available from measurements of individuals of unknown age in a chain owing to the impossibility of distinguishing the age groups. Investigations employing known individuals, such as Orton's (1914) constitute the only practicable method of obtaining reliable information upon growth rates, particularly of older individuals. During 1948 and 1949, a few *Crepidula* spat settled upon glass and Tufnol panels exposed at Burnham-on-Crouch in a general investigation of the season of settlement, rates of growth, etc., of sedentary marine organisms. These *Crepidula* were measured on the withdrawal of the panels. The sizes recorded lay between 10 and 22 mm.,[1] the panels having been exposed for two months (July and August) in each year. Such information must be interpreted with care, owing to the motility of the very young spat but these figures do represent the rates of growth in shell length of individuals from the time of initial settlement under favourable conditions, upon flat surfaces. As the length of a *Crepidula* shell is dependent upon the size and shape of the substratum, linear dimensions constitute poor criteria of shell growth, and an increase in length can only be considered an indication of growth.

## SUMMARY

The breeding of *Crepidula fornicata* from the Blackwater oyster beds was investigated during 1946 and 1947. A few observations were also made at Burnham-on-Crouch in 1948, 1949 and 1950. The methods of sampling, presentation of the results, and of assessing the significance of the results statistically are described.

In 1946 and 1949, developing embryos were found from April until early September, giving a breeding period of about 5½ months' duration. The intensity of spawning was similar in both years.

In 1947, spawning commenced shortly after the sea temperature had risen to and above 50° F. Observations made in 1948 and 1950 confirmed this.

A suggestion of periodic concerted spawning of the female *Crepidula* was obtained in 1946 and 1947. The results suggest that there is an irregular periodic spawning at or immediately after neap tides.

Observations strongly suggest that most female *Crepidula* spawn at least twice in a season.

Estimates are given of the duration of embryonic and larval life. At the beginning of the breeding period, embryos develop to the pre-veliger stage in about 14 days, and to veligers in 14–21 days hatching in 21–28 days. A tentative estimate of the duration of larval life of *c.* 35 days is made. The effect of temperature on embryonic development is discussed.

The sequence of spawning in the chain is considered at the beginning and

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[1] For example, on a glass panel exposed 12 July 1949 and withdrawn 9 September 1949, were two *Crepidula*, one 11 mm. and the other 22 mm. in length.

the end of the breeding period. There is some evidence that the older females spawn a little in advance of the younger ones.

The incidence of females (throughout the season) with a rudimentary penis is considered.

The mean number of females per chain at Tollesbury and West Mersea, and during and at the end of the spawning period, is discussed.

The settlement and growth of the spat of *Crepidula* are briefly described, and discussed.

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# STUDIES IN THE BIOLOGY OF TALITRIDAE (CRUSTACEA, AMPHIPODA): EFFECTS OF ATMOSPHERIC HUMIDITY

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(Text-figs. 1–9)

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## RESISTANCE TO DESICCATION

Although the high-water Talitridae are normally terrestrial they show little structural modification compared with aquatic amphipods. They have no obvious adaptations to limit water-loss, and their branchial method of respiration is typically aquatic. It was to be expected, therefore, that the evaporating power of the air would play a considerable part in limiting their habitats and determining their habits. The following experiments were made to try and assess the importance of this factor.

### *Apparatus and Methods*

A series of experiments was carried out to measure the survival times of *Talitrus saltator* (Montagu), *Talorchestia deshayesii* (Audouin) and *Orchestia gammarella* (Pallas) at different controlled humidities. Attempts were first made to control the humidity using saturated solutions of salts. The apparatus consisted of a glass dish, 18 cm. diameter by 7 cm. deep, divided horizontally by a copper-gauze platform of 0·25 mm. mesh. Beneath the platform were three dishes of diameter 5 cm. containing the solution; above it was an 'Edney' paper hygrometer. A Perspex lid, with central, corked hole for introducing animals, was sealed on to the dish with plasticine. When the air in the chamber reached equilibrium with the saturated solution, as shown by a steady hygrometer reading, animals were introduced. This, however, usually caused a considerable rise in the humidity. For example, at 15° C. using saturated magnesium chloride solution, the hygrometer reading rose from the equilibrium value (58%) to 70% R.H. in 15 min. on introducing three *Talitrus* and three *Orchestia gammarella*.

Besides showing the ineffectiveness of the method, this result shows the importance of the hygrometer as a humidity check, a precaution omitted by Backlund (1945) who measured the survival times of several animals, including *O. gammarella*. His apparatus gave a similar surface of saturated salt solution to mine, and he introduced ten specimens at a time. His results are considered later.

In the final form of the apparatus much more constant humidities were obtained by using sulphuric acid solutions in place of saturated salt solutions; the liquid surface was greatly increased by covering the whole floor of the chamber with solution, and the number of specimens in the apparatus was limited to six at a time (two of each species). The densities of the sulphuric acid solutions were measured with a hydrometer, and the equilibrium humidities were calculated from data contained in the International Critical Tables (National Research Council, U.S.A., 1926). The experiments were carried out in a constant temperature room at 25° C. Under these conditions the greatest variation in the hygrometer reading during any experiment was a rise of 5% R.H. after introducing specimens into a humidity of 36% R.H. At higher humidities introduction of specimens caused smaller rises in the hygrometer reading, and at 88% R.H. and above no rise could be detected.

Adult specimens of each species were transferred direct from laboratory stocks to the constant humidity apparatus, and survival time was measured from their introduction until no movement occurred, even when the animal was touched with a covered wire (insulated flex) through the hole in the lid.

### *Results and Discussion*

In all three species the first noticeable effect of desiccation was a failure to co-ordinate the limb movements, and a tendency to fall on one side. Later there was a darkening of the extremities of the limbs and antennae, particularly in *Orchestia*. The survival times are shown in Table I. In saturated air all specimens were healthy after 24 hr. After 48 hr. those of *Talorchestia deshayesii* were dead, but the others were healthy. None of the species can withstand even small saturation deficiencies for more than a few hours, but *Talitrus saltator* always survives considerably longer than the others. This may be due to its greater size and consequent smaller surface: volume ratio, yet at all humidities the survival times of *Talorchestia deshayesii* and *Orchestia gammarella* are almost identical, in spite of the much greater size of the latter.

It was found that in air of 36% R.H., in which adult specimens of *Talorchestia deshayesii* survived 75 min., juveniles of *T. saltator* and *Orchestia gammarella* of approximately the same size as an adult *Talorchestia deshayesii* both survived only 45 min.

'If the relationship between rate of water loss...and saturation deficiency is linear and survival is limited only by water loss, then the curve of longevity against saturation deficiency is hyperbola-shaped' (Johnson, 1942). The linear relationship between saturation deficiency and the reciprocal of longevity (Fig. 1) makes it reasonable to assume that, in the species under consideration, survival is limited only by water-loss, and that the rate of water-loss is not controlled by the animal. If this is the case, then the relationship between survival and saturation deficiency will be independent of the temperature, as has been shown to hold approximately true for several species of insect (Buxton, 1932; Johnson, 1942; Ludwig, 1945). On this assumption it is possible to compare the survival times obtained by the writer for *Orchestia gammarella* with those given by Backlund (1945). At a supposed humidity of 86% at 20° C. he obtained survivals of from 9 to 32 hr. This humidity corresponds to a saturation deficiency of 2·46 mm. Hg, under which conditions the survival time, from Fig. 1, would be 5 hr. Similar discrepancies occur at both higher and lower humidities, Backlund always obtaining much the greater survival time. This must be attributed to the method of humidity control he employed, using saturated salt solutions, which, as mentioned earlier, I found to be quite ineffective.

TABLE I. SURVIVAL TIMES OF *TALITRUS SALTATOR*, *ORCHESTIA GAMMARELLA* AND *TALORCHESTIA DESHAYESII* AT DIFFERENT CONTROLLED HUMIDITIES. TEMPERATURE, 25° C.

| Humidity (R.H. %) | Survival times (hr.) | | |
|---|---|---|---|
| | *T. saltator* | *O. gammarella* | *T. deshayesii* |
| 100 | >48 | >48 | >24 |
| | >48 | >48 | >24 |
| 95 | 16·0 | 9·0 | 9·0 |
| | 14·5 | 8·0 | 8·0 |
| 88 | 7·5 | 5·25 | 4·5 |
| | 7·0 | 4·5 | 3·5 |
| 75 | 5·0 | 2·5 | 2·5 |
| | 4·75 | 2·5 | 2·5 |
| 57 | 2·5 | 1·5 | 1·5 |
| | 2·5 | 1·5 | 1·5 |
| 36 | 1·75 | 1·5 | 1·25 |
| | 1·5 | 1·0 | 1·25 |

The animals in the above experiments had no access to food, which is normally plentiful in the habitats of all three species. Similar experiments were therefore made in which food was available, to determine whether Talitridae can utilize water in their food, or produced by its oxidation, to counteract water-loss by evaporation. Dry foods, in the form of (1) biscuit, (2) dextrose and (3) dried *Fucus* frond, were left untouched by both *Talitrus* and *Orchestia gammarella*, so that the role of metabolic water could not be determined. With moist foods it was difficult to avoid raising the humidity in the chamber on introducing the food, but no rise in the hygrometer reading occurred in the following two cases:

I. At R.H. = 95%, $T = 18°$ C., a piece of *Fucus serratus* frond measuring 6 × 1 cm. was provided as food. The wrack was dry to the touch, but flexible and not dried out. Three specimens of *Orchestia gammarella* were introduced. After 72 hr. one was dead, but the other two were healthy, and a considerable quantity of the wrack had been eaten.

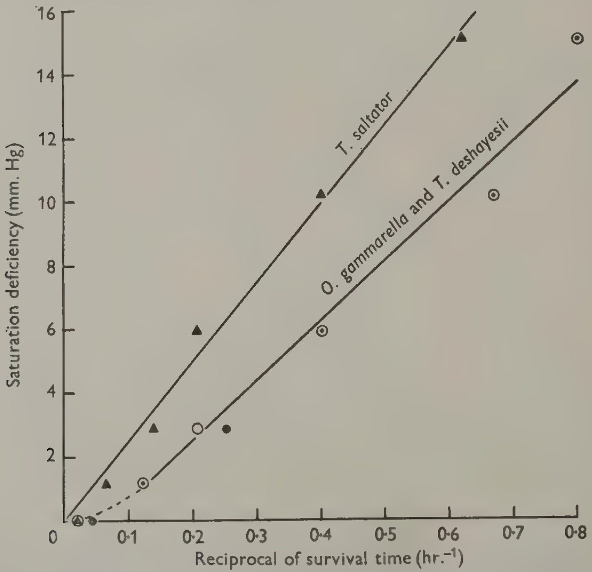

Fig. 1. Reciprocal of mean survival time plotted against saturation deficiency. ▲, *Talitrus saltator*; ○, *Orchestia gammarella*; ●, *Talorchestia deshayesii.*

II. At R.H. = 88%, $T = 25°$ C., a 1 cm. cube of *Drosophila* medium (Darlington & La Cour, 1942) was introduced into the chamber. Two normal specimens of *Orchestia gammarella* survived 20 and 22·5 hr. respectively. Two other specimens were introduced after first coating their mouthparts with paraffin wax to prevent them from feeding. One of these succeeded in removing the wax after 2 hr., and immediately began feeding. It was still healthy when the other died after 8 hr. All these specimens kept close to the food, usually touching it, and must have been in a local humidity appreciably higher than the general humidity of the chamber, the survival time of the waxed specimen being the same as that at 95% R.H. in the absence of food. Nevertheless, the greatly increased survival times of the specimens which fed suggests that water from food can play a very important part in enabling Talitridae to resist the effects of desiccation.

Field observations on the habitats and habits of the animals provide confirmation of the importance of food in this connexion. Backlund (1945) states that the humidity in the surface layers of wrack beds is at or near saturation only for a period of less than 4 hr. at night, and may fall well below 50% R.H. by day, and that the humidity of deep layers, though always high, is not always maximal. My own observations, made by immersing a paper hygrometer in different wrack beds for periods of over 30 min., at depths of about 15 cm., have shown humidities from 85 to 90% R.H. These readings were always made when *O. gammarella* was present in the wrack in the vicinity of the hygrometer. The humidity of the normal habitat of *O. gammarella* is, therefore, such that in the absence of food the animal would die of desiccation in a few hours, and *Talorchestia deshayesii*, with similar resistance to desiccation, inhabits even drier situations. In another section of his work, Backlund comments on the great amounts of food consumed by *Orchestia gammarella*, 'but the amount of excrements is also great and most of the stuff eaten is not utilized'. I have noticed that talitrids always pass dry faeces, even when feeding on very moist food, suggesting that the amount of food eaten is determined by the animals' water requirements rather than their energy requirements.

*O. gammarella* is normally found among wrack on a non-sandy substratum, and *Talorchestia deshayesii* among, or under, wrack on a sandy substratum. Both species feed both by day and by night, and seldom wander far from the wrack, though they do come into the open more at night. A contrast is found in the behaviour of *Talitrus*, which feeds little by day but remains buried beneath the sand, often many yards away from the nearest wrack. At night it ranges over the beach from the lower slopes of sand dunes, well above high-water spring level, to mid-tide level or as low as the sea permits. These long periods without food by day and long migrations over the exposed beach at night probably could not be sustained by the other two species because of their much smaller resistance to desiccation.

## Orientation in Humidity Gradients

As talitrids are very susceptible to desiccation even at high humidities, it seemed important to investigate their behaviour when a choice of humidities is available to them, to find to what extent, and by what means, they can distinguish between moist and dry air, and to compare the reactions of the different species. Experiments were made on the same three species for which the resistances to desiccation were compared, namely *Talitrus saltator*, *Orchestia gammarella* and *Talorchestia deshayesii.*

### *Apparatus and Methods*

To produce humidity gradients, a form of Gunn & Kennedy's 'alternative' chamber was used (Gunn & Kennedy, 1936). The apparatus measured 18 cm. diameter by 7 cm. deep, and the platform was of copper gauze of 0·25 mm. mesh. Resting on the platform were two 'Edney' paper hygrometers, one on either side of the chamber, with the sensitive paper in each case to the outside, and the edge of each instrument 1 cm. from the edge of the chamber to allow a clear path for the animals round the perimeter.

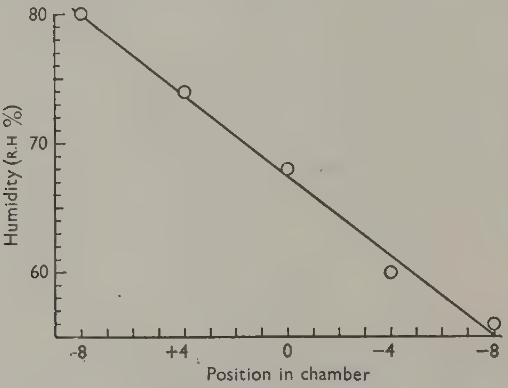

Fig. 2. Typical humidity gradient in 'alternative' chamber. Humidities at 1 cm. from edge of chamber. Temperature, 15° C.

The calibration of the hygrometers was checked at intervals of about a month over sulphuric acid solutions of measured density, and they were checked against each other at air humidity every few days so that any variation in the calibration of either instrument would have been detected. The calibration never varied by more than 2% R.H. in any month.

In the majority of cases the dishes beneath the platform contained sulphuric acid solutions of different strengths, but caustic soda and caustic potash, both solid and solution, and solid calcium chloride were used in several of the experiments with similar results to those obtained with sulphuric acid at similar humidities, showing that the animals were reacting to the humidity gradient and not to any property of the desiccating agent.

By placing the desiccating agent in two well-separated dishes an approximately linear gradient of humidity was obtained. A typical gradient is shown in Fig. 2. If each half of the floor of the chamber is covered with dishes, meeting at the boundary of the moist and dry halves, a much steeper gradient is obtained in the boundary region, with a very gradual gradient on either side (such an arrangement was used by Gunn (1937), who includes an S-shaped graph of a typical gradient under these conditions). While animals are likely to give a more obvious response to the steep gradient, the nature of the response is likely to be seen more clearly in a linear gradient where reactions will not be confined to the boundary region.

The platform was marked with a diameter, dividing the chamber into moist and dry halves, and with lines parallel to this diameter at 2 cm. intervals. With the aid of these lines the distances of animals from the diameter could easily be estimated to the nearest centimetre, such distances in the moist half being regarded as positive and in the dry half as negative, so that the position of an animal could be referred to by a number between +9 and −9.

Up to 3 hr. was required for equilibrium to become established in the chamber. Specimens were not introduced until the hygrometers had been showing steady readings for at least half an hour. Only one specimen was introduced into the chamber at one time, and numerical values of the intensity of reaction to the gradient were based on the respective times spent by the animal in each half of the apparatus. In most of the previous work on the behaviour of animals in humidity gradients using an 'alternative' chamber, several specimens have been introduced at once, and measures of intensity of reaction based on readings of the number of animals in each half (Gunn, 1937; Gunn & Cosway, 1938; Pielou & Gunn, 1940; Lees, 1943). This method gives greater uniformity of results, since each result is an average for several specimens, but it cannot be applied to Talitridae because of their high rate of water-loss. Not only does the introduction of several talitrids noticeably affect the humidities in the chamber, but, particularly at low humidities, the steepest gradients leading to the moistest air surround the animals themselves. It was found in several preliminary experiments using five to ten specimens of *Orchestia gammarella* that all the specimens soon formed an aggregation round any stationary individual irrespective of its position in the chamber.

Young specimens of all species jump much more frequently than do adults, making it very difficult to plot their positions accurately. For this reason specimens below a size roughly corresponding to that of sexual maturity were avoided (9 mm. for *Talitrus*, 8 mm. for *Orchestia gammarella* and 6 mm. for *Talorchestia deshayesii*, all lengths with abdomen flexed). Apart from this no conscious selection was made.

The apparatus was always illuminated from directly above, and, to allow for any visual orientation of the specimen to external objects, the chamber was turned through 180° half way through each set of observations. On first introducing specimens, they would frequently feign death for periods of over a minute or show unusually great activity with much jumping. To allow them to become acclimatized to their surroundings no observations were recorded for the first 5 min. after introduction.

Position records (Figs. 3–6) were obtained by noting the displacement of the animal from the diameter at 15 sec. intervals (shown by open circles on the graphs), and positions of additional turning points were also recorded (shown by black circles).

As a measure of the intensity of reaction to the humidity gradient the 'excess percentage time' was used, i.e.

$$\frac{(\text{time spent in moist half}) - (\text{time spent in dry half})}{(\text{time spent in moist half}) + (\text{time spent in dry half})} \times 100,$$

which gives a theoretical range of values from + 100 %, representing an animal which does not leave the moist half, to − 100 %, representing an animal which does not leave the dry half, with 0 % representing no preference. Intensities were normally calculated from observations over two periods of 8 min. each, the apparatus being turned round between the two periods. With a few, large, fast-moving specimens of *Talitrus*, observations were confined to two periods of 5 min. each, while with a few slow-moving specimens of *Talorchestia deshayesii*, observations were continued for 10 or even 12 min. in each period. In all cases the average time for one complete circuit of the chamber was less than 3 % of the total time for which observations were recorded. Intensities of reaction were calculated either from position records or, more usually, from observations on the times when the specimen crossed from one half to the other.

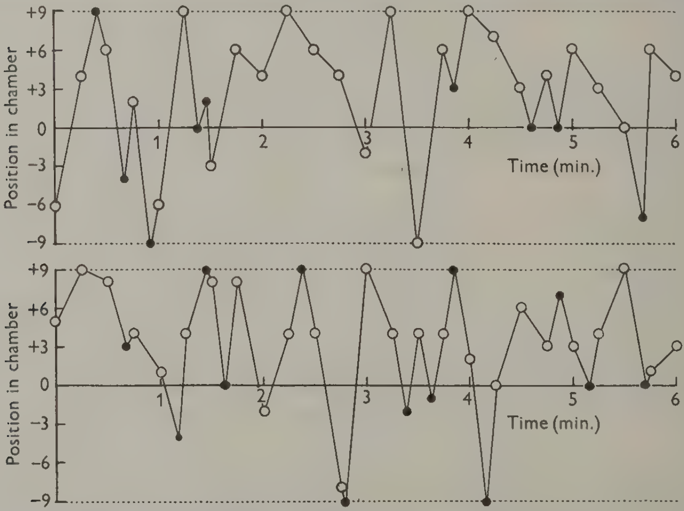

Fig. 3. Position record of *Talitrus saltator* in humidity gradient 92–38 % R.H. at 16° C. The apparatus was turned through 180° between the upper and lower records. ○, positions at 15 sec. intervals; ●, positions of additional turning points.

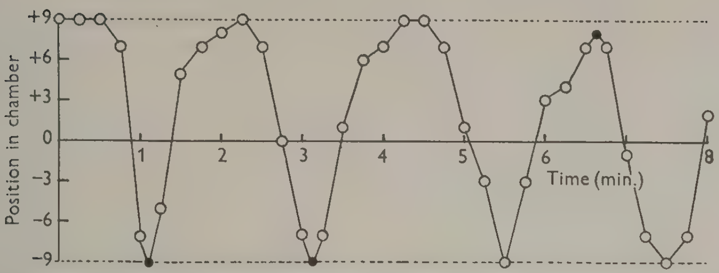

Fig. 4. Position record of *Orchestia gammarella* in humidity gradient 86–66 % R.H. at 15° C.

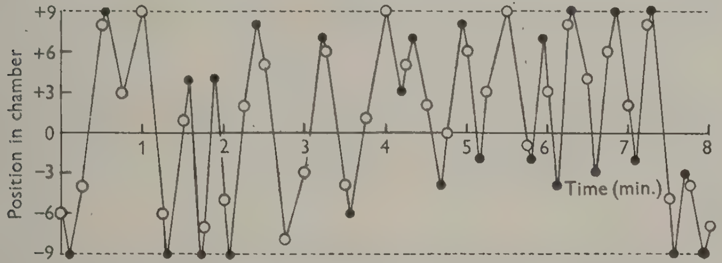

Fig. 5. Position record of *Orchestia gammarella* in humidity gradient 76–50 % R.H. at 16° C.

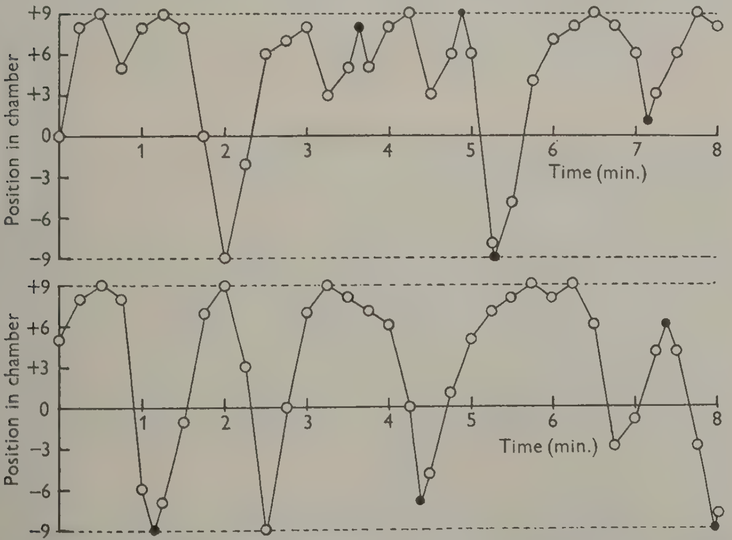

Fig. 6. Position record of *Talitrus deshayesii* in humidity gradient 96–78 % R.H. at 15° C. The apparatus was turned through 180° between the upper and lower records.

All experiments were made at temperatures between 14° and 16·5° C.

Control experiments, in which the humidity was the same on both sides of the chamber, were made for all three species. Intensities of reaction greater than twice the standard deviation in control experiments for each species were regarded as significant.

### *Significant Reactions*

The minimum significant intensities for *Talitrus saltator*, *Orchestia gammarella* and *Talorchestia deshayesii* are, respectively, 13, 5 and 15. The low figure for *Orchestia gammarella*, compared with the other two species, is the result of its stronger thigmo-taxis. While in control experiments this species almost invariably followed a single track round the perimeter of the chamber, the other two occasionally left the sides and wandered over the platform. The theoretical maximum deviation from zero intensity of an animal which moves round the perimeter at a uniform rate without turning is the percentage time taken for one circuit of the chamber. This value for an average *O. gammarella* over two 8 min. periods is estimated at about 3%, and this value was seldom exceeded in control experiments for the species. The less restricted paths followed by *Talitrus saltator* and *Talorchestia deshayesii* resulted in greater variation in controls.

### *Preferred Humidities*

In over 250 experiments on the three species, at humidities from 25 to 100% R.H., all the significant reactions were positive. This means that whenever talitrids show a humidity preference it is for the highest humidity available, up to, and including, saturated air. The preferred humidity is therefore the same as the optimum humidity as judged by survival times.

### *Types of Orientation*

In this paper, orientation reactions are named according to the system described by Fraenkel & Gunn (1940).

All three species are thigmo-tactic, and tend to keep to the outside of the chamber with one antenna against the glass wall. This behaviour is most strongly marked in *Orchestia gammarella* which seldom leaves the outer wall, and therefore follows a restricted course. The other two species more frequently forsake the perimeter for the open platform.

Examination of position records (Figs. 3–6) shows that talitrids spend most of their time in moist air as the result of two factors: (i) the animals do not move at a constant speed, and (ii) they do not move in a constant direction.

#### *Changes in Speed*

The animals move more quickly in dry than in moist air. This is shown, to some extent, in all the position records, but Fig. 4 shows a specimen of *O. gammarella* whose hygro-positive reaction results entirely from this type of orientation. Movement at a constant speed round the perimeter of the chamber would give a sinusoidal graph, but the differential velocity of the specimen results in broad peaks and narrow, more pointed troughs. This orientation is an example of 'low hygro-ortho-kinesis' (Fraenkel & Gunn, 1940).

(It is probable that the stimulus in the case of talitrids and several other species which react to differences of humidity is not humidity but rate of water-loss. The conventional practice of describing such orientations in terms of humidity is followed here, but to describe them in terms of evaporation would be more correct.)

Two variants of hygro-ortho-kinesis are sometimes shown by talitrids:

(*a*) When the highest humidity in the chamber exceeds about 90% R.H., animals will frequently stop in the more humid regions and remain motionless for up to 30 sec. Halts in the drier regions are extremely rare and seldom exceed 5 sec. This reaction is shown by all three species, but is most common in *O. gammarella*.

(*b*) At lower humidities (less than about 50% R.H.) the animal may start jumping and will continue jumping until it lands in moister air, when walking is resumed. The jumping is quite random in direction, but usually three or four jumps are sufficient to take the animal out of the drier region. Though this reaction has been seen in all three species, it is most common in *Talorchestia deshayesii* and least common in *Talitrus saltator*.

Variant *a* is an extreme case of variation in the velocity of locomotion, while *b* involves variations not only in velocity but also in the type of locomotion. Both are examples of greater locomotor activity in drier air or low hygro-ortho-kinesis.

### *Changes in Direction*

In Fig. 3, 5 and 6 turning reactions play a very important part in the hygro-positive behaviour of the specimens; they turn more frequently when moving from moist to dry air than when moving from dry to moist air. Turns are not always made towards moister or away from drier air, in fact, in some cases, turns towards drier air are almost as frequent as those towards moister air (e.g. Fig. 5). The hygro-positive reaction results from the intervals between turns tending to be relatively shorter when the animal is moving into drier air, or, as Ullyott (1936) found with flatworms in a gradient of light intensity, 'an increase in stimulating intensity produces an increase in the rate of change of direction'.

As the animals usually follow the outer wall of the chamber, turns are usually complete reversals of direction, and the direction of locomotion is not truly random. The restrictions in the direction of locomotion are, however, not imposed by the humidity, but by the tendency of the animals to keep close to projecting objects (thigmo-taxis). As far as the humidity gradient is concerned the direction of locomotion is random. This is seen more clearly when specimens temporarily leave the outer wall of the chamber—behaviour only very occasionally seen in *Orchestia gammarella*, but more common in *Talitrus saltator* and *Talorchestia deshayesii*. On the open platform the undirected nature of the turning reaction is very obvious. It does not result (except by chance) in motion towards or away from the source of the stimulus (evaporation), and is not governed by the direction of the humidity gradient, but by comparisons of the intensity of the stimulus at successive times. By a 'process of alternate stimulation and adaption the animal is gradually brought to the weaker end of the gradient' (Ullyott, 1936). The orientation is clearly of the same type as that shown by *Dendrocoelum* in a gradient of light intensity, described by Ullyott under 'phobotaxis', and later re-named 'klino-kinesis' by Fraenkel & Gunn (1940).

In very steep humidity gradients talitrids will occasionally stop when moving into dry air, then move backwards for about 1 cm. before turning. Comparable behaviour is common in *Paramecium* when moving into unfavourable conditions, and has been included under klino-kinesis by Gunn & Walshe (1941). A similar type of reaction is frequently shown by wireworms in steep gradients of humidity, but was regarded by Lees (1943) as a directed reaction, and therefore described as 'klino-taxis'. However, his own figures show that neither the direction of recoil nor the direction of the track after turning bore any relation to the direction of the gradient, the direction of recoil being determined solely by the original path of the wireworm, and the new path frequently leading the animal back into dry air almost immediately.

True klino-kinesis as a reaction to humidity gradients is shown by the beetle, *Tenebrio molitor*, which shows a preference for dry air (Pielou & Gunn, 1940). The orientation involves 'trial movements with the antennae...followed by a fairly precise movement towards the dry side'. Nothing comparable with this type of reaction appears to occur in wireworms or talitrids whose turning reactions in humidity gradients are properly described as 'klino-kinesis'.

Normally talitrids orientate in humidity gradients by a combination of ortho-kinesis and klino-kinesis, though weaker reactions may consist solely of ortho-kinesis (as in Fig. 4). The relative importance of the two types of reaction varies considerably between different individuals in the same gradient, but no consistent differences in this respect were noticed between different species or between different sizes or sexes of the same species.

### *Intensities and Limits of Reaction*

The intensities of reaction of similar specimens of the same species in the same humidity gradient often differ enormously; for example, with a gradient 98–71% R.H. at 15° C. three different specimens of *Orchestia gammarella* gave intensities of 17, 30 and 74% excess time. These individual differences do not appear to be correlated with size, sex or previous desiccation. In spite of this lack of uniformity in the intensities of reaction of different individuals, there is consistency in the reaction of different specimens of the same species; for if one specimen is found to react to a certain gradient then, in general, all other specimens of the species will react to the same gradient, and if no reaction is given by one specimen then all other specimens will fail to react. This makes it possible to make quite a sharp distinction between those humidity gradients to which members of each species will react and those to which they will not.

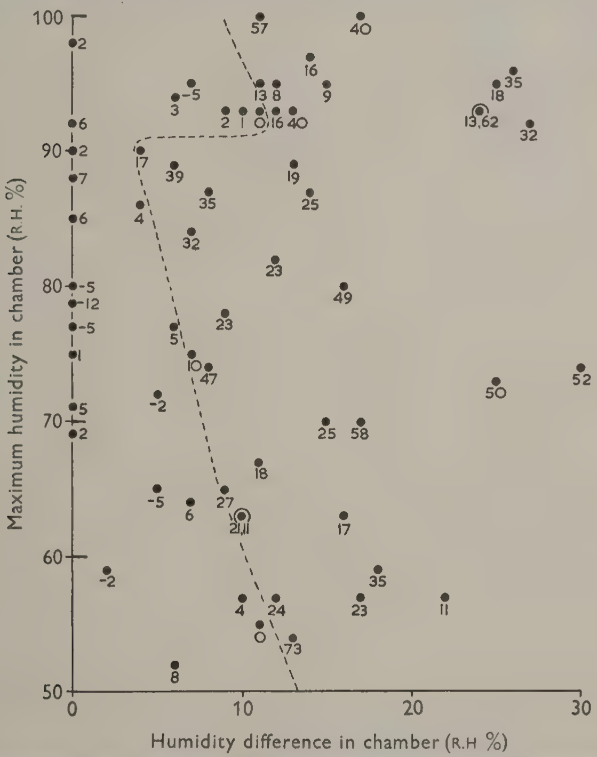

Fig. 7. Intensities and limits of reaction of *Talitrus saltator* to humidity gradients in 'alternative' chamber. Figures beside points give intensities of reaction. Circles around points denote that two or more experiments have been made using the same humidity gradient. The broken line marks the approximate limit of significant reaction. Temperature, 14–16·5° C.

This is done in Figs. 7–9. The free-hand dotted line in each case divides those gradients to which the vast majority of reactions were significant (on the right) from those to which the vast majority were not significant (on the left). (The limits of significance for each species are given, and differences in their value are discussed, earlier.)

The minimum humidity difference required to give a significant reaction varies at different parts of the humidity range, and the manner in which it varies differs with the species. Thus *Talitrus saltator* gives a significant reaction to a humidity difference of 4% R.H. when the highest humidity in the chamber is 90%, but humidity differences of over 10% R.H. are required to obtain a reaction when the maximum humidity is above 92% or below 60% R.H.

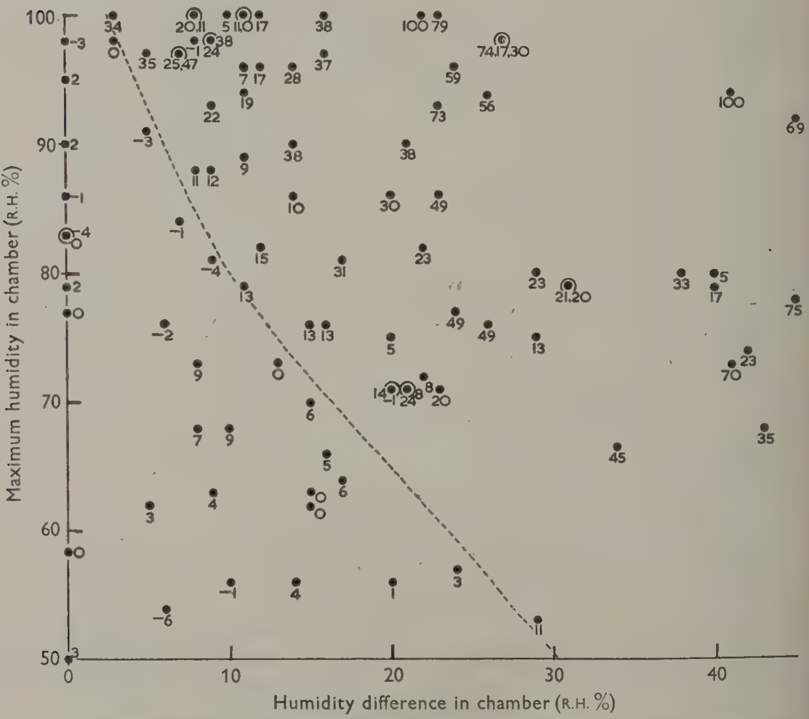

Fig. 8. Intensities and limits of reaction of *Orchestia gammarella* to humidity gradients in 'alternative' chamber. Temperature, 14–16·5° C. For further explanation see Fig. 7.

(Fig. 7). *Orchestia gammarella* is most sensitive to small humidity differences when the maximum humidity is 100% R.H., when it shows a significant reaction to a humidity difference of 3% R.H., but its sensitivity decreases steadily with decreasing humidity (Fig. 8). *Talorchestia deshayesii* reacts to a 5% R.H. difference when the maximum humidity is between 60 and 65% R.H., but its sensitivity decreases rapidly at lower, and more gradually at higher, humidities (Fig. 9).

In all three species there is no uniform increase in intensity of reaction with increasing humidity gradient, either considering results over the whole humidity range or any section of it. This might be attributed to the large individual differences mentioned earlier, but corresponding values for *Porcellio* (Gunn, 1937) show the same feature in spite of the averaging effect of using several (five) specimens in each gradient. Values for *Agriotes*, on the other hand, increase steadily with increases in both the humidity gradient and the maximum humidity (Lees, 1943).

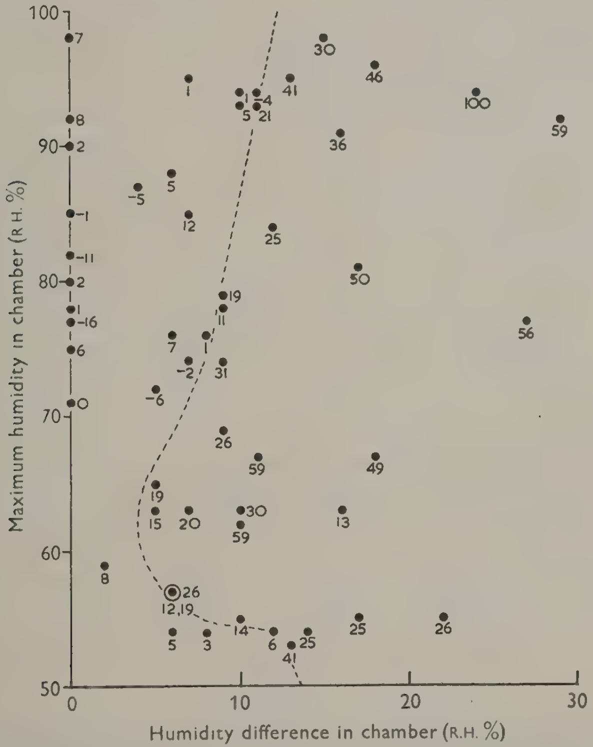

Fig. 9. Intensities and limits of reaction of *Talitrus deshayesii* to humidity gradients in 'alternative' chamber. Temperature, 14–16·5° C. For further explanation see Fig. 7.

Specific differences among talitrids in the humidity zone in which they are most sensitive can be related to their field behaviour to a considerable degree. *Talitrus saltator* is unable to distinguish between different humidities above 92% R.H. This figure probably represents the lowest humidity at which it can safely spend its day-time, non-feeding period, and it seems significant that its greatest sensitivity should be shown at humidities just below this value. It is probable, as mentioned earlier, that the humidity reaction of talitrids depends on their ability to compare different rates of water-loss, which is governed by saturation deficiency. A relative humidity of 92% at 15° C. corresponds to a saturation deficiency of 1·02 mm. Hg, under which conditions (from Fig. 1) an adult *Talitrus* would survive over 20 hr. It is therefore suggested that *Talitrus* may use its humidity sense in determining the depth of its burrow, but the humidity in the burrow is not known.

*Orchestia gammarella* is the only species which inhabits the deeper layers of wrack beds where humidities are at or near saturation, and it may use its great sensitivity at high humidities to keep in this environment. To quote Backlund (1945), 'the humidity gradation is steep in the border horizon between deep layers and surface layers [of wrack beds]. Here many animals can use their humidity sense directly'.

The humidity zone in which *Talorchestia deshayesii* reacts to the smallest humidity differences lies at what must be the extreme lower limit of its environmental humidity range, but this species frequently lives in this humidity zone where mistakes in judging humidities might soon lead to desiccation, so that an efficient humidity sense is vital. The resistance of *T. deshayesii* to desiccation is almost identical with that of *Orchestia gammarella*, yet *Talorchestia deshayesii* is almost invariably found in drier situations. When the two species are found together in the same wrack bed, as frequently occurs at the mouths of estuaries, it is very noticeable that in dry weather *Orchestia gammarella* occupies the moist, deep layers, while *Talorchestia deshayesii* inhabits the dry, surface layers. *Orchestia gammarella* invades the surface layers only when the air humidity is high, as at night.

The humidity in wrack strings on sandy beaches is probably very similar to that in the surface layers of wrack banks. Here, too, *Talorchestia deshayesii* is to be found feeding by day and by night, but at night it is joined by *Talitrus saltator*. Thus, by living at the lowest humidities at which it can survive, *Talorchestia deshayesii* by day avoids competition for food with both *Orchestia gammarella* and *Talitrus saltator*.

### *Humidity Receptors*

Attempts were made to locate humidity receptors in *Talitrus saltator* and *Orchestia gammarella* by amputating appendages or insulating different parts of the body from the atmosphere with wax or vaseline, and observing such specimens in humidity gradients. Specimens treated in the following ways were observed in a gradient of 95–70% R.H.: (i) *Talitrus saltator* with antennae amputated; (ii) *Orchestia gammarella* with antennules and antennae covered with vaseline; (iii) *Talitrus saltator* with head, mouthparts, antennules and antennae covered with wax; (iv) *Orchestia gammarella* with dorsal surface covered with wax; and (v) *Talitrus saltator* with dorsal surface and thoracic legs covered with vaseline.

All these animals showed well-marked preferences for moist air, orientating in the same manner as untreated specimens. Attempts were also made to cover the under surfaces of the animals with wax, vaseline or cellulose paint, but in all cases the specimen was either killed or completely immobilized. No doubt the covering of the branchiae had a pathological effect.

Gunn (1937) showed that covering the antennae of *Porcellio* with vaseline did not affect its humidity reactions, and suggested that receptors might be present on the thorax. Lees (1943) showed by amputation that in wireworms the antennae, labial palps and maxillary palps were all concerned in humidity reception, but he found no specific organs of reception. This, together with the discovery that the animals reacted to differences in saturation deficiency rather than relative humidity, led him to suggest that the reaction was initiated by loss of water from the head appendages, and in particular from the unsclerotized, intersegmental regions. These two animals are the only normally hygro-positive species which have been investigated previously for humidity receptors, and in neither case has any receiving organ been found. In view of this, and because I have been unable to locate the site of humidity reception in talitrids, I suggest that their reactions to humidity are brought about by evaporation from the whole body surface, and particularly from the thin-walled branchiae which probably lose water more rapidly than the rest of the body.

Organs of humidity reception have been located and identified in the hygro-negative *Tenebrio* (Pielou & Gunn, 1940), and *Pediculus* (Wigglesworth, 1941). In both cases they are situated on the antennae. It has also been suggested that certain of the antennal hairs of mosquitoes are hygro-sensitive (Thomson, 1938). In all these cases the organs are thought to act like hygrometers, and in the case of the mosquito it has been shown that the intensity of the humidity reaction depends on the gradient of relative humidity and not on differences in saturation deficiency. Animals which react to humidity differences appear, therefore, to fall into two distinct classes: (*a*) those with hygrometer-like receptors, which react to differences in relative humidity, and (*b*) those with no specific receptors, which react to differences in rates of evaporation. The Talitridae fall in the second category.

This work was carried out at King's College, Newcastle-upon-Tyne, under the supervision of Prof. A. D. Hobson, whom I wish to thank for advice and encouragement.

## SUMMARY

The survival times of *Talitrus saltator*, *Orchestia gammarella* and *Talorchestia deshayesii* were measured at different controlled humidities.

All are very susceptible to desiccation, but *Talitrus saltator* survives much longer than either of the other species in unsaturated air in the absence of food.

Survival times are greatly increased if moist food is available.

In humidity gradients all species select moist air, orientating by means of an ortho-kinesis and a klino-kinesis.

At 15° C., *T. saltator* reacts to the smallest gradients when the maximum humidity is 92 % R.H., but is unable to distinguish between different humidities above this figure. *Orchestia gammarella* and *Talorchestia deshayesii* react to the smallest gradients when the maximum humidities are 100 and 62 % respectively.

Attempts to locate humidity receptors were unsuccessful. The animals are thought to react to rate of water-loss from the whole body.

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# STUDIES IN THE BIOLOGY OF TALITRIDAE (CRUSTACEA, AMPHIPODA): VISUAL ORIENTATION IN *TALITRUS SALTATOR*

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(Text-figs. 1–4)

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## ORIENTATION BETWEEN TIDEMARKS

The nocturnal migrations of *Talitrus* over the sand surface cover considerable distances, frequently taking specimens well below mid-tide level. In spite of this, by day the species occupies burrows in a broad, but fairly well-defined, zone in the region of high-water mark. The nocturnal distribution of the animals can be attributed to a somewhat random search for food, but the question arises (worded anthropomorphically), how do the animals find their way back to the high-water region? Perhaps in an attempt to answer this question, Verwey (1929) states briefly that *Talitrus* orientates on the beach by mnemotaxis to the wind, sun and direction of the sea, and by menotaxis (compass reaction). Mnemotaxis, or orientation by memory images, has been entirely eliminated from the modern classification of orientation reactions (Fraenkel & Gunn, 1940), so that Verwey's contribution is reduced to a statement without evidence that *Talitrus* orientates by means of a compass reaction to an unknown stimulus, and no other author mentions the orientation of *Talitrus* on the beach.

When, by day, specimens of *Talitrus* are taken from their burrows and released on firm sand between tidemarks, they will, either immediately or after a period of up to 3 min. apparently random wandering, take up a straight course towards high-water mark. Typical examples are shown in Fig. 1*a*, which, like other figures in this section, was drawn from freehand records of the animals' paths. Distances were gauged by pacing. Progress is made both by walking and jumping. When an animal jumps it usually turns in the air, and is seldom still pointing towards high-water mark on alighting, but it immediately aligns its body with its former course before continuing. Small deviations are made towards pebbles or other objects projecting from the sand. Pebbles are not detected beyond half a metre, but the animal moves towards larger objects at greater distances, including the observer at up to 3 m. (In practice, therefore, the animals were observed from beyond this range.) Unless the *Talitrus* burrows, it soon continues on a course parallel to that previously followed. It burrows on encountering a piece of sand where the surface is broken, as at a worm-cast or a foot-print, or, eventually, on reaching the less tightly packed sand at high-water mark. A specimen has been observed to follow a straight course over 80 m. in length to high-water mark.

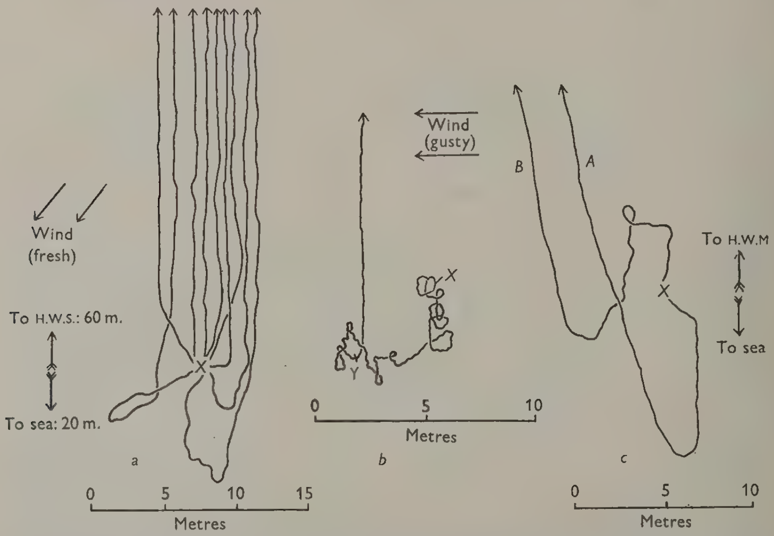

Fig. 1. *a*, tracks of nine *Talitrus saltator* released singly at *X* on a sandy beach; *b*, track of a specimen released at *X* with eyes painted (eyes cleaned at *Y*); *c*, tracks of (A) a normal adult male *Talitrus* released at *X* and (B) a similar adult male with right eye painted, released at same point.

This orientation has been confirmed in several dozen specimens of *Talitrus* on five different sandy beaches in Northumberland. Courses usually run at right angles to high-water mark, but occasionally, though straight, they are at a slight angle to the normal. All animals released at the same point follow approximately parallel courses.

A compass reaction to the sun or wind could only take place if the animal reached its inter-tidal position by following a certain course, and returned on a reciprocal bearing. The behaviour of *Talitrus* was shown not to be an example of this type of orientation by carrying animals from their place of capture to their release point in a covered container. Such animals orientated in the normal way. Animals collected from different points along the beach, or which had been kept in captivity for several days, all followed parallel courses from the same release point, showing that the reaction is not homing behaviour. The orientation was found to be uninfluenced by the position of the sun in the sky, or by overcast conditions, or by the direction of the wind. Strong winds would at times blow animals some distance along the beach, but on regaining their feet they would take up a course parallel to that previously followed.

That the animals did not make use of the slope of the beach was shown by releasing specimens on a raised sandbank and on an undulating surface; tracks were always towards high-water mark whether leading downhill, level or uphill. There was in no case any gradient or discontinuity of salinity, moisture or humidity that the animals could have followed, and the orientation appeared too rapid and too accurate to be due to any of these factors.

It was noticed that orientating animals always held the antennae outstretched sideways with the tips on the sand. From this it was thought possible that these appendages were acting as receptors to some directional stimulus, perhaps vibrations from the sea, but the orientation was clearly shown by animals whose antennae had been amputated.

The possibility of a visual orientation was tested by using animals whose eyes were painted with a mixture of glue and indian ink. Such specimens showed no trace of a directional orientation (Fig. 1*b*). This not only showed that the orientation was visual, but confirmed the inability of the animals to make use of the slope of the beach. Previous observations that the orientation was independent of the position of the sun showed that it was not a simple light reaction; it therefore appeared that form-vision was involved. The fact that the orientation was not destroyed in unilaterally blinded specimens (Fig. 1*c*) confirms that a light-balance between the two eyes is not involved. If such had been the case, unilateral blinding would have led to circus movements. Fig. 1*c* also gives an example of tracks which are not perpendicular to high-water mark.

Animals released from such a position that their direct route to high-water mark was barred by water, showed a normal orientation until within about 2 m. of the water, when they turned and ceased to follow a straight path (Fig. 2). This suggests that, although water can be detected at short range, the tracks of the animals towards high-water mark cannot be the result of orientation away from the sea. This is confirmed by watching orientating animals, which, when walking, follow a straight course without turning the body, yet the position of the eyes makes it quite impossible for them to see the sea.

The fact that all tracks from the same release point tend to run parallel all the way to high-water mark suggests that orientation is to some distant object, beyond high-water mark. Considering the range at which *Talitrus* detects objects on the beach (such as pebbles and man) the only suitable objects, large enough to be detected, which are normally present are sand dunes or other features composing the skyline. Orientation to the highest point on the skyline does not explain all observed cases, nor has any feature yet been detected which can be regarded as directing the orientation.

It seems, at first sight, improbable that form-vision plays an important part in directing the reactions of a nocturnal animal, yet there are very few summer nights when a silhouette of the sand dunes against the sky is not visible to man from the beach, and *Talitrus* may have better night vision than man. Some evidence for infra-red vision in *Talitrus* is provided by the fact that several specimens showed the normal inter-tidal orientation in a fog which limited human vision to about 200 m., and the peaks of the nearest sand dunes were about 250 m. from the release point. Even if *Talitrus* is unable to use this orientation at night, it could still be of great importance, for the general return to the high-water region probably takes place at dawn.

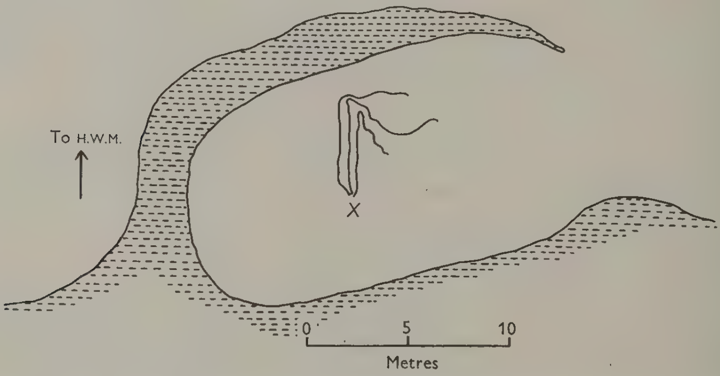

Fig. 2. Tracks of three *Talitrus saltator* released on a sandbank almost surrounded by water.

The inter-tidal orientations of other talitrids have not been studied in the same detail as those of *Talitrus*, but a few observations have been made on *Talorchestia deshayesii*, *Orchestia gammarella* and *O. mediterranea*.

*Talorchestia deshayesii* appears to show similar reactions to *Talitrus*, but, owing to its small size and the necessity of standing at least 3 m. away from the specimen, it is soon lost to view, and when jumping it is influenced much more by the wind than is *Talitrus*.

The reactions of the species of *Orchestia* on a rocky beach would be likely to have important bearings on their natural behaviour, but the abundance of cover among rocks makes the observance of such reactions very difficult. Bate & Westwood (1863) state that when *O. mediterranea* is disturbed it always jumps towards the sea, but I am unable to confirm this. As far as can be observed, both this species and *O. gammarella* scatter in all directions.

Observations have been made on a number of *O. gammarella* released on sand. Specimens released within about 100 m. of rocks made straight towards the rocks. Of specimens released well away from the rocks, one consistently made straight towards the sea in several tests. This reaction was destroyed by painting the eyes. Other specimens followed courses away from the sea, which, though fairly straight, did not run parallel.

While further observations are necessary before forming any conclusions about the visual orientation of *O. mediterranea* and *O. gammarella* in nature, it seems that *Talitrus*, and probably also *Talorchestia deshayesii*, makes use of some feature of the skyline in returning to high-water mark from between tidemarks.

## LABORATORY EXPERIMENTS

Having obtained strong evidence that *Talitrus* makes use of form-vision in nature, laboratory experiments were designed to investigate the ability of the animals to distinguish between different shapes, and, if possible, to obtain further information about their visual responses.

Before proceeding further, some explanation of the use of the term 'telo-taxis' is necessary. It has been described by Fraenkel & Gunn (1940) as 'orientation to a source of stimulus, as if it were a goal', and implies the direct attainment of orientation without a balance of intensities of stimulation. The difference between this type of reaction and balance reactions (tropo-taxis and klino-taxis) is seen when two sources of stimulation are present; an animal orientating by a balance reaction will then make between the two (assuming a positive reaction), while an animal orientating by telo-taxis will make towards one and ignore the other, though if the two sources are of similar intensity it may frequently switch its orientation from one to the other, giving a zig-zag path. Such a zig-zag path is associated with telo-taxis alone.

Fraenkel & Gunn 'restrict the term "taxis" to a reaction in which the stimulus is undifferentiated and does not involve form-vision', and, as an extension of this rule, apply the term 'telo-taxis' to certain reactions to light only. Cases in which animals react to shapes by the same orientation (e.g. *Carcinus*, *Eupagurus*) are excluded from the category on the grounds that 'the reaction is...rather too complex to be called a taxis'. Although form-vision is a more complex process than the detection of light, the orientation, in examples such as *Carcinus* and *Eupagurus*, is no more complex than photo-telo-taxis; in fact, if the stimulus were unknown, the two could not be differentiated. Telo-taxis is the description of a particular type of orientation, and as such it must include all examples of this type of orientation, whatever the stimulus. Certainly more complex forms of orientation should be excluded from telo-taxis, but it is not a description of stimuli. For these reasons I have used the term 'telo-taxis' in the following pages to refer to *any* reaction in which 'orientation in the direction of the source of stimulation occurs without balance' as if to a goal (Fraenkel & Gunn, 1940).

### *Apparatus and Method*

For investigating the visual orientation of *Talitrus*, apparatus was used as shown in Fig. 3. An animal placed on a horizontal blackboard, measuring 6 × 4 ft. (1·85 × 1·23 m.), could see a vertical white screen or the projections thrown upon it at one end of the board, but was screened from direct light from the projector. The figures for the projections were painted in indian ink on blank lantern slides. Specimens were released from under an inverted jar so that the experimenter could not influence the direction in which they faced at the time of release. As the animal crawled on the board the observer marked its track with chalk. As long as the hand and chalk were kept behind the specimen it showed no reaction to them.

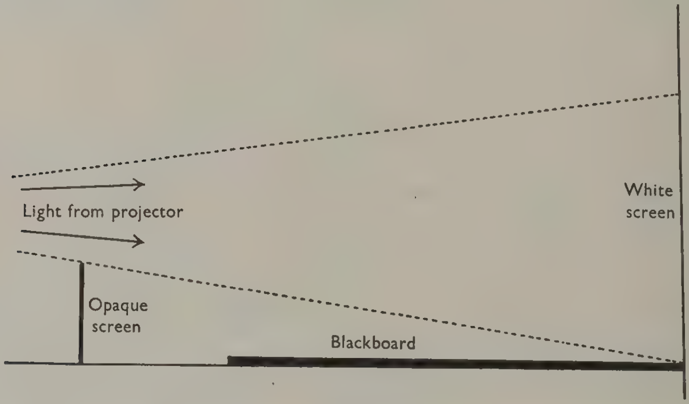

Fig. 3. Arrangement of apparatus for studying visual orientation in *Talitrus saltator*.

*Orchestia* and *Talorchestia* are much less suitable than *Talitrus* for use with this apparatus. Being smaller, they are less easy to see and less easy to handle, and they show effects of desiccation more quickly. They also jump a great deal more than *Talitrus* so that their courses cannot be plotted as accurately. Experiments were therefore confined to *Talitrus*. Adult specimens of both sexes were used.

In Fig. 4 the projection on the vertical screen is shown directly above the tracks of the specimen on the horizontal blackboard. All tracks in the same figure refer to the same specimen, released at different points (marked $X$). In general, different figures refer to different specimens.

### *Results and Discussion*

When first removed from beneath the sand in laboratory cultures, specimens of *Talitrus* usually show a photo-negative reaction, but, if kept in the light, the orientation changes to photo-positive within 10 min. Such photo-positive animals were used in the following experiments. When confronted with an illuminated, white screen (Fig. 4*a*) they made towards it, but followed no very direct path, nor did the tracks end near any particular point on the screen. A similar, rather inaccurate, photo-positive reaction was shown when much of the screen was darkened so as to give a black-white, vertical boundary (Fig. 4*b*), and when the projection was a white square (Fig. 4*c*). In these three cases the animals orientate towards the light, and there is no suggestion of form-vision.

The reaction to a large, illuminated rectangle (Fig. 4*d*) shows quite a different orientation from the inaccurate photo-positive behaviour already seen. The tracks are more direct, and most of them are towards one or other of the upright boundaries of the rectangle, sometimes changing from one to the other to give the zig-zag path which characterizes telo-taxis. The sources of stimulus for the telo-tactic reaction are not light sources, but the vertical dark-light boundaries. The reaction cannot be explained except as a case of form-vision though the shape of an upright line is as simple a form as can be imagined. Three of the seven tracks (and part of one of the other four) are not in the direction of these objects, but only in the general direction of the screen. In these cases the specimen is showing the photo-positive behaviour seen in Fig. 4*a–c*.

Telo-taxis to a vertical dark-light boundary is even more clearly shown to the projection of two light squares (Fig. 4*e*). Here none of the reactions are to light; they are all to the shape of the upright edges. The fact that most of the tracks end at the edge of the right-hand square was probably the result of this square being slightly the more brightly illuminated.

Orientation to a more complex shape is seen in Fig. 4*f*, *g*. In both cases the animals make towards the foot of an incline. With several different specimens it was found that with the single slope (Fig. 4*f*) the majority of the tracks led directly to the foot of the incline when the angle $a$ was between 15 and 70°, but beyond these limits the tracks were not precisely directed, but were examples of the inaccurate photo-positive orientation illustrated in Fig. 4*a–c*. Similarly, with the projection shown in Fig. 4*g*, well-directed responses were obtained when $a_1 = a_2 = 15°$ or bigger, but only occasional tracks led to the foot of the slopes when $a_1 = a_2 = 10°$.

Comparison of Fig. 4*h*, *i* shows that the directed orientation to a downward taper is not given to an upward taper.

Again, using the projection of two squares shown in Fig. 4*e*, but with one coloured red and the other green, or red and blue, similar tracks were obtained to those using white light. While not revealing any colour preference on the

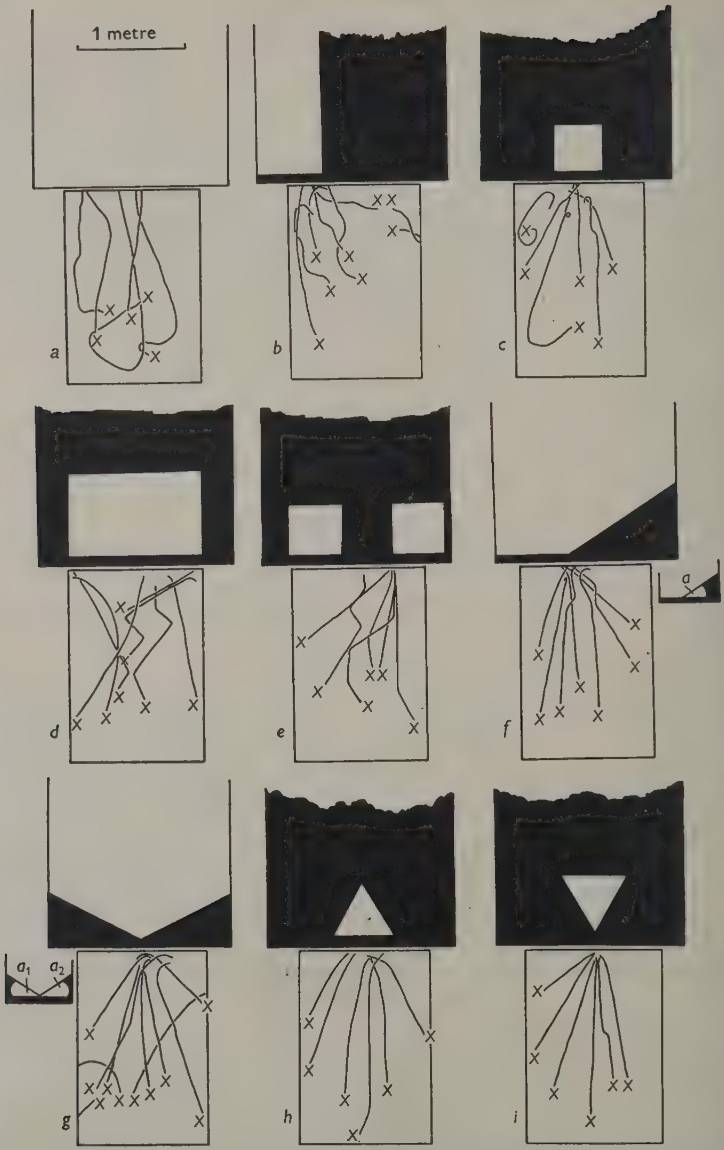
1 metre
a
b
c
d
e
f
a
g
$a_1$
$a_2$
h
i

Fig. 4. Visual orientation in *Talitrus saltator*. The upper part of each figure shows projection on vertical white screen; the lower part shows tracks of specimens released at $X$ on the horizontal board.

part of the animals, or demonstrating colour vision, it shows that all three colours are within their visual frequency range.

It has not been possible to link the laboratory behaviour of *Talitrus* to specific shapes with its orientation on the beach, but the laboratory experiments have confirmed beyond doubt the conclusion drawn from the beach experiments that *Talitrus* is capable of form-vision and shows a positive orientation to certain shapes.

I am indebted to Prof. A. D. Hobson for advice and encouragement in this work, which was carried out at King's College, Newcastle-upon-Tyne, under his supervision.

## SUMMARY

*Talitrus saltator* placed on firm sand, between tidemarks, in daylight, usually follows a direct course to the high-water region.

The orientation is visual, and probably involves form-vision of distant objects.

Form-vision in *Talitrus* was demonstrated in the laboratory by its reaction to silhouettes. It makes towards the foot of an incline and sometimes towards a vertical, dark-light boundary.

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# PHOTOGRAPHY OF THE SEA FLOOR

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(Plate I and Text-figs. 1–2)

## Introduction

During the last sixty years many attempts have been made to take photographs underwater at depths varying from just below low-water to many thousands of feet. The pioneer work of Boutan (1893) showed clearly that the essential requirements were a relatively light apparatus fitted with a good source of illumination. Ewing, Vine & Worzel (1946) gave a list of workers who have obtained underwater photographs at wading or diving depths. In their own work Ewing, Vine & Worzel have designed a number of underwater cameras with which they have taken some thousands of pictures of the sea-bottom. In their free-floating cameras the apparatus is allowed to sink to the bottom with a ballast weight. On touching the bottom a trigger sets off the camera which takes two pictures with a time interval of 30 sec. After this the ballast is released and a float brings the apparatus to the surface. In their suspended cameras the component parts are mounted, as in the free-floating cameras, on a vertical pole, with the camera near the top and a trigger at the base. Activation of the camera occurs when the trigger touches the bottom. Their most satisfactory light source proved to be the photoflash bulb. With one or other of these cameras they have obtained large numbers of clear photographs in depths ranging from 10 to 2400 ft., and have used these in studies of bottom deposits, sand ripples, and the distribution of animal life. (See also Ewing, Woolard, *et al.*, 1946.)

In the present work an attempt has been made to design and construct an underwater camera which will serve as a tool for estimating the density of the larger bottom-living invertebrates on the trawling grounds (in depths of 50–80 m.) near Plymouth. The essential requirement was a large number of workable pictures taken at known positions in a limited area. It was decided that photo-flash bulbs would not be suitable, for although they would give a small number of high-quality pictures at each lowering of the camera, they could not be used to produce a large number of consecutive pictures at a single lowering. Up to the present it has not been possible to work with an electronic flash as light source, but Ewing, Vine & Worzel (1946) found that, except in shallow water, the cable losses are so high and the cable itself so heavy that they considered it impractical to use lengths of more than 150 ft. (*c.* 50 m.). It would, of course, be possible to put the supply and conversion unit into a pressure-proof container and lower them with the camera, but this would make the whole apparatus very inconvenient to handle at sea. It was, therefore, decided to use a battery of photoflood lamps as a source of light for the present apparatus, and this has proved relatively successful.

## ACKNOWLEDGMENTS

I am much indebted to Mr F. J. Warren who designed and installed the electrical circuits and the control box, to Mr F. G. C. Ryder who was responsible for the construction and assembly of the underwater mechanical components, to Captain C. A. Hoodless, D.S.C., and the crew of R.V. *Sabella*, whose skill and patience have enabled the apparatus to be operated efficiently at sea, and to Dr D. P. Wilson and Mr G. M. Spooner for their guidance and assistance in photographic and statistical methods respectively.

## DESCRIPTION OF THE APPARATUS

The arrangement of the underwater components is shown diagrammatically in Text-figs. 1 and 2. The camera is mounted near the top of a vertical metal tube. The lamps are arranged asymmetrically round a metal ring attached to the pole at a height of 0·65 m. from the bottom of the pole. The foot switch is mounted in the base of the pole. Between the foot switch and the attachment of the lamp ring to the pole there is a gun-metal junction box for the electrical leads.

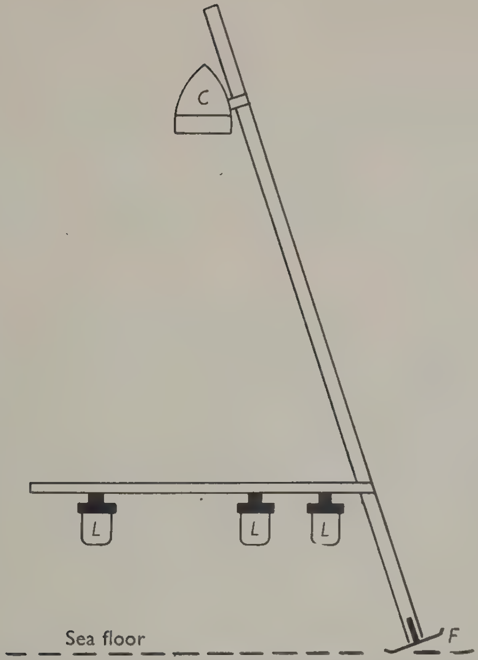
The camera used is a Robot II fitted with a Zeiss Tessar 3·75 cm. lens. The camera switch is depressed by a solenoid mounted behind the camera and activated by the foot switch.

The camera case is of gun-metal and is fitted with $\frac{1}{2}$ in. plate-glass window. The case is closed by the compression of a round rubber ring in the joint between the base of the case and the dome. The compression is by a 'samson' with a single $\frac{1}{2}$ in. bolt bearing down on the summit of the dome.

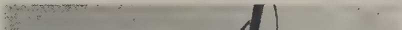
In its present form the apparatus has six 500 W. photoflood lamps, each mounted in a cast aluminium alloy base and enclosed in a standard glass dome. The junction between the glass and the metal is made by grinding a surface on to the edge of the glass with carborundum powder, and then seating this ground glass surface on to the metal base with a little vaseline. The glasses are held in position by a wire 'samson', but the actual sealing is effected by the pressure of the water on the glass dome.

The foot switch consists of a 21 cm. diameter brass plate connected by a socket joint to a small sealed metal bottle containing a mercury switch. When the foot touches the bottom it is driven upwards and inverts the mercury switch which activates the solenoid in the camera case.

Power from the ship's mains (200–210 V.) is supplied to the junction box near the base of the pole by a 7-core rubber-covered cable. From the junction



Text-fig. 1. Side view of underwater photographic apparatus at the moment when a picture is taken. (Lights shown on one side of the ring only.) *C*, camera case; *L*, lamps; *F*, foot and foot switch.



Text-fig. 2. Photograph of the underwater camera, showing camera, ring of lamps and junction box. The foot and foot switch are out of the picture at the bottom.

box four leads go to the lamps and two connect the foot switch and the camera solenoid; the seventh core is not used.

On deck the power is led through a control box before entering the main electric cable. This box is fitted with fuses for the camera and lamp circuits and for the ship's power supply, and with switches and ammeters for the camera and light circuits. It also has a counter which records the number of pictures taken and a buzzer which rings when a picture has been taken.

## OPERATION OF THE CAMERA AT SEA

The Robot camera is loaded with a metre length of 35 mm. high-speed film and is fitted into the camera case, which is then securely closed. The ship is stopped and a lead sounding gives the depth in metres. The apparatus is then lowered on a wire warp led over the aft boom to the main winch. When the camera is 3–5 m. from the bottom the speed of lowering is reduced, the lamps are switched on and the lamp ammeter in the control box gives a reading. At the same time the camera switch in the control box is switched on, and as soon as the foot touches the bottom the camera circuit is completed, the first picture is taken and the film is automatically wound on. When this happens the camera ammeter in the control box gives a reading and at the same time the counter clicks on to record the number of the photograph, and the buzzer rings to warn the crew that bottom has been reached. The winch is stopped immediately and the apparatus is then lifted from 1 to 2 m. off the bottom by hand hauling on the warp.

The ship is allowed to drift for a known interval of time, and the camera is again lowered steadily to take the second picture. This procedure is repeated until the whole film has been used up (40–45 exposures). The time interval between each exposure can be varied according to the speed of drift of the ship, but it is usually of the order of 30 sec., so that a film of 40 exposures can be taken in 20 min.

One of the main advantages of this method of operation is that it is possible to plot with reasonable accuracy the location of each photograph on a large-scale chart of the area. To do this it is only necessary to know the positions and times of the first and last pictures, and the time interval between each exposure.

## PRELIMINARY RESULTS

It was found that the most satisfactory method of interpreting the photographs and counting the larger invertebrates was by examining the negatives under a binocular dissecting microscope. When there were large concentrations of animals on a single frame counting was facilitated by the use of some form of grid. Using this method of interpretation in conjunction with a micrometer slide it was possible to obtain size measurements of the animals counted. The following preliminary results on the density and distribution of bottom-living animals in four areas near Looe and Plymouth were obtained from the examination of 479 photographs, each covering 1 m.$^2$ of the bottom. The figures obtained for the size of each animal will be given in a later paper.

### *Area of Station* L 4 (Pl. I).

This station is mid-way between Plymouth breakwater light and the Eddystone. Photographs were taken along the following three transects:

| Date | Start of transect | End of transect |
|---|---|---|
| 7. vii. 49 | ½ mile W. of L4 | ¾ mile W. of L4 |
| 24. viii. 49 | Rame Head, 005° T., 3·7′ | Rame Head, 050° T., 4·8′ |
| 8. viii. 50 | Eddystone, 200° T., 3·0′ | Eddystone, 200° T., 4·0′ |

The bottom in this area was muddy sand with small patches of gravel and shell debris, often lying in pockets. Trawl catches in recent years have repeatedly suggested that the epifauna of this area is poor, and this is confirmed from an examination of photographs representing 83 m.$^2$ of bottom. An analysis of the numbers of each species found in this area is given in Table I, which also records comparable figures for the other three areas surveyed. The only large invertebrates recorded more than once on any transect in the L 4 area are *Asterias rubens*, *Ophiura texturata* and *Chlamys opercularis*. The figures for *Asterias rubens*, although small, suggest that this species is rather unevenly distributed at a rate of not more than one individual to every 10 m.$^2$, while *Chlamys opercularis* is perhaps a little more abundant. The only other invertebrate found in any number is *Cellaria*, the figures given for this bryozoan denoting clumps of about 20 cm. in length. In two of the three transects there are numbers of holes, *c.* 1·3 cm. diameter, probably formed by tubicolous worms or burrowing molluscs or crustaceans.

### *Area south and south-west of Eddystone.*

Photographs were taken along the following two transects:

| Date | Start of transect | End of transect |
|---|---|---|
| 16. viii. 49 | Eddystone 360° T., 2·0′ | Eddystone 360° T., 3·0′ |
| 23. x. 50 | Eddystone 019° T., 3·2′ | Eddystone 030° T., 4·3′ |

The bottom in this area is clean sand, and in 1947–48 trawling records showed a rich and abundant population of *Asterias rubens* feeding on *Chlamys opercularis* (Vevers, 1949). Trawl catches in this area during 1949 and 1950 have shown a marked decrease in the numbers of these species, although the individuals of *Asterias rubens* are still large in size. A total of 122 clear photographs (= 122 m.$^2$) shows the paucity of both *A. rubens* and *Marthasterias glacialis* in 1949 and 1950 (Table I). *Chlamys opercularis* appears to be still relatively abundant, at a rate of about one individual to 2 m.$^2$. There was no sign of *Cellaria* on these grounds, although another, unidentified, bryozoan (or ? sponge) occurred occasionally. A few specimens were recorded of unidentified burrowing sea anemones.

TABLE I. NUMBERS OF ANIMALS IDENTIFIED ON UNDERWATER PHOTOGRAPHS, 1949–50.

| Locality ... ... | Area of L 4 (muddy sand with small patches of gravel) | | | S. and S.W. of Eddystone (clean sand) | | S.E. of Looe Island (muddy sand and gravel with pebbles) | | | S.W. of Looe (muddy sand and gravel with pebbles) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Date ... ... ... ... | 7. vii. 49 | 24. viii. 49 | 8. viii. 50 | 16. viii. 49 | 23. x. 50 | 30. vi. 50 | 7. vii. 50 | 26. vii. 50 | 5. x. 49 | 2. viii. 50 |
| Mean depth (m.) ... ... | 55 | 52 | 55 | 69 | 70 | 50 | 50 | 48 | 46 | 54 |
| Number of pictures (each 1 m.$^2$) ... ... ... | 23 | 44 | 16 | 34 | 88 | 91 | 21 | 53 | 72 | 37 |
| Species: | | | | | | | | | | |
| *Callionymus* sp. | — | — | — | 1 | — | — | — | — | — | — |
| *Asterias rubens* | 4 | 3 | 1 | — | 1 | 5 | 3 | 1 | 3 | — |
| *Marthasterias glacialis* | — | — | — | 1 | 2 | 2 | — | — | 2 | — |
| *Porania pulvillus* | — | 1 | — | — | — | — | — | — | — | — |
| *Astropecten irregularis* | — | — | — | 2 | 1 | 3 | 1 | — | — | — |
| *Palmipes membranaceus* | — | — | — | — | — | 1 | — | — | — | — |
| *Echinus esculentus* | — | — | — | — | — | — | — | — | 2 | — |
| *Ophiura texturata* | 1 | 3 | — | 10 | 7 | — | — | — | — | 1 |
| *Ophiocomina nigra* | — | — | — | — | — | — | — | — | 2 | — |
| *Ophiothrix fragilis* | — | — | — | — | 26 | — | — | — | 18 | 1280* |
| *Pecten maximus* | — | — | — | — | — | 16 | — | 1 | 12 | 1 |
| *Chlamys opercularis* | 5 | 5 | 1 | 35 | 30 | 14 | — | — | 3 | 17 |
| *Turritella communis* | 1 | — | — | — | — | — | — | — | — | — |
| *Eupagurus prideauxi* | — | 1 | — | — | 3 | 1 | — | — | 2 | — |
| *Portunus depurator* | — | — | — | — | — | 1 | — | — | — | — |
| Crab sp. | — | 1 | — | — | — | 2 | — | — | — | — |
| *Hyalinoecia tubicola* | 1 | — | — | — | — | 1 | — | — | — | — |
| *Cellaria* sp. | 5 | 23 | — | — | — | 2 | — | — | — | — |
| *Lepralia foliacea* | — | — | — | — | — | — | 5 | — | — | — |
| Bryozoan (or sponge) | — | — | — | 6 | 1 | 6 | — | — | — | — |
| Sea anemone spp. | — | — | — | 2 | 1 | 5 | — | — | — | — |
| Hydroid spp. | 2 | — | — | — | — | 4 | — | — | — | — |
| Depressions *c.* 4·4 cm. diam. | — | — | — | — | — | 5 | 9 | 27 | — | — |
| Holes *c.* 1·3 cm. diam. | — | 29 | 71 | — | 4 | 463 | 134 | 294 | 526 | 77 |

* The 1280 specimens of *O. fragilis* were actually present in 12 only of the 37 m.$^2$ interpreted.

*Area south-east of Looe Island.*

Photographs were taken along the following three transects in 1950:

| Date | Start of transect | End of transect |
|---|---|---|
| 30. vi. 50 | Looe Island 328° T., 3·7′ | Looe Island 328° T., 4·7′ |
| 7. vii. 50 | Looe Island 326° T., 3·4′ | Looe Island 318° T., 4·0′ |
| 26. vii. 50 | Looe Island 337° T., 3·4′ | Looe Island 316° T., 2·3′ |

The bottom was mainly of muddy sand and gravel with pebbles in some parts. The distribution of invertebrates on the bottom was variable, only the films taken on 30 June 1950 showing any large number of individuals. On this transect starfishes (*Asterias rubens*, *Marthasterias glacialis* and *Astropecten irregularis*) were present in small numbers. The large scallop, *Pecten maximus*, was relatively abundant, when compared with its frequency on other grounds, while the queen scallop, *Chlamys opercularis*, was far less abundant than on the clean sand area south of Eddystone. Sea anemones and hydroids also appeared to be more numerous than on the other grounds, and in one film there is a short length showing clumps of the polyzoan *Lepralia foliacea*. However, the most striking feature of all three transects in this area is the high number of holes made by the infauna (*c*. 1·3 cm. diameter) similar to those found in the L 4 area. In addition, there were patches of ground showing smaller numbers of irregular wide-mouthed depressions about 4·4 cm. diameter. These depressions were similar to those produced at the anterior end of some polychaete burrows. Further work, including larger scale pictures, dredge or grab hauls in the area, and experiments in the laboratory will be required before the occupants of these and the smaller holes can be identified.

*Area south-west of Looe Island* (Pl. I).

Photographs were taken along two transects:

| Date | Start of transect | End of transect |
|---|---|---|
| 5. x. 49 | Looe Island 025° T., 4·6′ | Looe Island 035° T., 4·8′ |
| 2. viii. 50 | Looe Island 013° T., 4·9′ | Looe Island 360° T., 5·5′ |

The bottom deposits were, in general, similar to those in the area south-east of Looe Island, consisting of muddy sand and gravel with pebbles. The two photographic transects available for this area show quite different features. The first transect (5 October 1949), consisting of 72 m.$^2$, is similar to the transect taken south-east of Looe Island on 30 June 1950. It has a number of the larger starfishes, as well as *Pecten maximus* and the unidentified holes (*c*. 1·3 cm. diameter); it only differs in the scarcity of queen scallops and in the presence of small numbers of *Ophiothrix fragilis*.

The second transect (2 August 1950) shows no starfishes, crustaceans or polyzoan colonies, but a very large population of *O. fragilis*, with a few queen scallops and occasional patches of ground with the unidentified holes (*c*. 1·3 cm. diameter). Twelve interpreted photographs in this transect yielded a count of 1280 *O. fragilis*. But the brittle star also occurred in large numbers in frames other than those counted, that is, they were present in the unclouded portions of the partly clouded frames. Examination of 33 successive photographs for the presence or absence of the brittle star gave the following result, the interval between each frame in this transect being approximately 10 m.:

TABLE II. OCCURRENCE OF *OPHIOTHRIX FRAGILIS* IN SUCCESSIVE PHOTOGRAPHS, 2 AUGUST 1950

| Serial numbers of photographs | Occurrence of *O. fragilis* (+ = present, – = absent, ? = doubtful) |
|---|---|
| 1891–93 | + |
| 1894–97 | – |
| 1898–99 | + |
| 2000 | ?+ |
| 2001–15 | + |
| 2016–17 | ? |
| 2018–20 | + |
| 2021–22 | ? |
| 2023–24 | + |

Taking that part of the transect covered by pictures 1898–2015 (inclusive), a sample of 18, there were 17 squares with *O. fragilis*, and one square doubtfully occupied by the same species. If, on a simple presence and absence basis, each one of a sample of 17 squares is found occupied, then it may be shown that there is a 95% chance that at least 83% of the squares of the sampled area (i.e. 170 m.$^2$) are occupied, or a 99% chance that at least 79% of the squares of the sampled area are occupied (since $0{\cdot}84^{17}$ gives a P of 0·95, $0{\cdot}83^{17}$ gives a P of 0·04, $0{\cdot}80^{17}$ gives a P of 0·023, and $0{\cdot}79^{17}$ gives a P of 0·018.)

However, since the number of individuals in the counted squares was large, varying from 38 to 206, the chances are even greater than this that all the squares in the sampled area were occupied, or, at any rate, that very few of the squares were unoccupied.

The total number of *O. fragilis* in the 12 fully interpreted and counted squares was 1280, giving a mean of 107 ± 14·7 individuals to the square metre. So that a transect of, say, 150 m. would have a total of 11,550–20,550 individuals.

In all the counts of *O. fragilis* on this transect the numbers recorded are minimum figures, for it is possible that in some patches individuals may have been obscured by those lying above them.

## DISCUSSION

Collections of animals from the sea-bed by means of dredge, otter trawl and Agassiz trawl give satisfactory qualitative samples of the epifauna. However, quantitative estimations by these methods involve errors owing to the impossibility of knowing the exact length of time during which the fishing gear has been on the bottom, and, in the case of the otter trawl, the lack of knowledge on the shape and size of the trawl mouth when in operation. Sampling of the bottom by means of grabs, such as that of Petersen (1918), or the scoop bottom sampler of Holme (1949) probably gives reasonably accurate results when used for the estimation of the infauna, but it is doubtful whether they give comparable results when used for the estimation of the larger epifaunal invertebrates, which are often sparsely distributed on the floor of the sea.

The use of an underwater camera to give photographs of a number of quadrats along a transect is similar in principle to the sampling methods used in extensive surveys of land vegetation (Tansley, 1923). The apparatus described in this paper is designed to obtain a succession of sample quadrats of known area at known intervals along a transect. The preliminary results from photographs of four different areas suggest that the method can be used as a competent and reasonably accurate tool, not only for the estimation of epifaunal invertebrates, which is its primary purpose, but also for counts of those infauna species which produce a tube or burrow with an opening on the surface of the sea-bed. Many photographs have been taken which show high densities of such burrowing animals. Counts of these burrows would help to confirm estimations made from the catches of bottom-sampling gear. Before this can be done, however, more information must be obtained on the shape, size and general appearance of these surface holes, so that the species producing them can be easily distinguished.

The number of photographs required to give an accurate estimate of the density of animals on a ground will clearly depend upon the nature of the bottom deposit and the type and habits of the species living there. On a poor ground, such as the L 4 area, or on a ground with heterogeneous bottom deposits, such as the muddy sand and gravel area south-east of Looe Island, a relatively large number of pictures, perhaps 300–500 $m.^2$ for 2–4 square miles in area, would be required in order to obtain a reasonably good estimate of animal density. In the latter ground there is considerable variation in the numbers and types of animals found along each of the three transects photographed.

The muddy sand and gravel area south-west of Looe Island also showed evidence of patchiness, the first transect being relatively poor in numbers of animals, while the second transect had an area which was very rich in one species only. In this latter transect, however, a small number of pictures showing homogeneous features was sufficient to enable definite conclusions to be reached on the extent of this local population of animals.

The presence of aggregations of brittle stars on localized areas of the sea-bed has long been suspected from the very large catches of these animals brought up by the dredge and Agassiz trawl. Nevertheless, the size of the aggregations, as estimated from the present photographs, is considerably greater than would be suspected from random dredge hauls. The existence of such large monospecific concentrations of animals raises a number of problems. Blegvad (1914) found that *O. fragilis* was essentially carnivorous. It is possible, therefore, that the brittle stars photographed were feeding on an extensive bed of animals, perhaps lamellibranch or other spat. Their massing behaviour might also be connected with spawning, and further photographs at different times of the year might provide further evidence on this point. The species is, in fact, known to be gregarious under laboratory conditions, and it is not uncommon for young specimens to be found clinging to adults rather in the fashion of the young of brood-protecting species. Their gregarious behaviour may not, therefore, be entirely related to food and spawning, and the individuals may react in a positive way to tactile, chemical or other stimuli produced by their fellows.

Although the quality of many of the photographs in the present series is by no means satisfactory, a sufficient number of them were clear enough for interpretation, and it is considered that larger scale pictures of an area smaller than 1 m.$^2$ would also yield useful results.

There are still a number of technical difficulties, in particular the provision of a continuous source of illumination adequate for a long series of pictures or even for a ciné film. These difficulties must, of course, be overcome without rendering the apparatus unwieldy.

There is little doubt that photography of the sea-bed can yield much information which will be of use in estimating the numbers of bottom-living animals, not only in inshore waters, but also in the offshore trawling grounds. There is also the possibility that use could be made of television to view the sea-bottom, and film records of the television screen would render permanent the results obtained by this method.

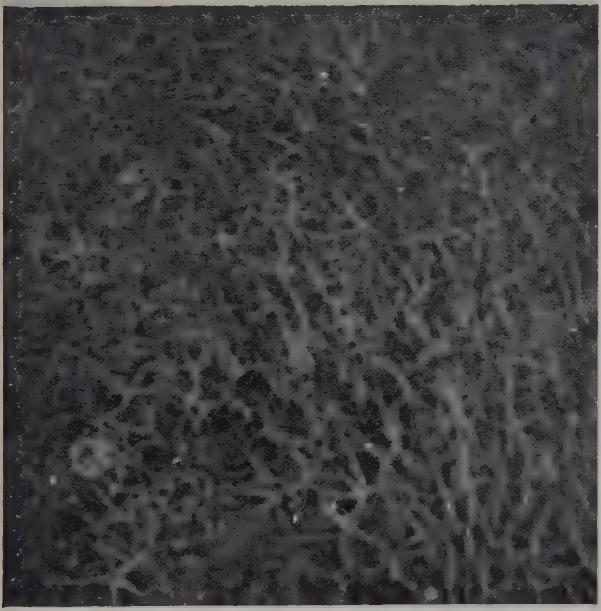
## SUMMARY

A description is given of an underwater photographic apparatus designed to take a transect of 40–50 exposures, each 1 m.$^2$, at depths up to at least 80 m. The camera used was a Robot II, and light was provided by six 500 W. photoflood lamps. Power was led from the ship's mains to the camera release and the lamps by a rubber-covered 15 amp. cable.

Photographs have been obtained of the sea-bottom on four different grounds near Plymouth and Looe, and from their interpretation a preliminary estimate has been made of the relative abundance of some of the larger bottom-living invertebrates in these areas. On some transects the sample photographs show a high density of unidentified holes made by members of the infauna.

On one transect a sample of 33 pictures showed a dense aggregation of the brittle star, *Ophiothrix fragilis*. This animal was present at the rate of $107 \pm 14{\cdot}7$ individuals to the square metre, and calculations have shown that the population was relatively homogeneous at this density over a distance of more than 100 m.

As the number of pictures taken at each lowering of the camera is relatively large it is considered that the photographic method described can be used to give a reasonably accurate estimate of the epifaunal invertebrates in known positions and at depth up to at least 70–80 m.



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## EXPLANATION OF PLATE I

*Above*: Photograph of 1 m.$^2$ of bottom near L4, showing one *Chlamys opercularis*, one *Ophiura texturata*, and also a patch of shelly gravel and (top right-hand corner) a large hole. Depth 55 m. *Below*: Photograph of 1 m.$^2$ of bottom, 5 miles south-west of Looe Island, showing dense mass of *Ophiothrix fragilis* lying on a bottom of muddy gravel. Depth 54 m.

# NOTES ON THE REPRODUCTION AND EARLY DEVELOPMENT OF THE CIRRATULID *THARYX MARIONI* (ST JOSEPH)

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(Text-figs. 1, 2)

The larval development of the Cirratulidae is not well known, although an account of the development of *Raphidrilus nemasoma* Mont. was published by Sokolow in 1911 (under the name of *Ctenodrilus branchiata*), and of *Audouinia tentaculata* (Montagu) by Wilson in 1936. Apart from these two publications, only scattered observations may be found in the literature, and these are listed by Wilson (1936). Unfortunately, attempts to rear the larvae of *Tharyx marioni* (St Joseph) beyond the hatching stage have failed, and as it seems unlikely that further data may be gathered for some time, such results as have been obtained are presented here.

The main points of interest in the development and reproductive habits of *T. marioni* are: (i) the adults are atoquous; (ii) the eggs are comparatively large and yolky, and unlike *Audouinia tentaculata*, the pelagic stage is omitted; and (iii) the larva on hatching is achaetous, as in other cirratulid larvae.

The worms and larval stages were collected from a small population at Chalkwell, Essex, on the north side of the Thames estuary, in fairly clean sand just above half-tide mark. The adults were buried vertically in the top few centimetres, entirely within the oxidized layer, and with the cirri exposed on the surface.

The morphology of the adults agrees well with the description given by Fauvel (1927) except that: (i) the sexually mature adults were never more than 35 mm. in length (Fauvel states the length to vary between 35 and 100 mm.); (ii) the adults were devoid of all pigment other than the red blood pigment (Fauvel describes them as 'reddish brown'); (iii) the ripe oocytes were colourless and appeared chalky white in the mass (Fauvel states that they are 'greenish').

I am indebted to Dr D. P. Wilson for kindly checking my identification.

## REPRODUCTION AND SPAWNING

It is impossible to distinguish the sexes with the naked eye. They do not differ in size, and when ripe both appear white due to the presence either of spermatozoa, or oocytes. The females, however, may be detected with a hand lens, as the oocytes may then be distinguished in the coelom. Males and females occurred in equal numbers. From a sample of thirty-seven worms, eighteen were females, nineteen were males.

The gametes are restricted to the mid-body region, being absent from the anterior region, and from the last few segments, in both sexes. Ripe females have about fifty genital segments, with a total number of between 1000 and 1500 oocytes.

Unfortunately spawning was not observed, but the oocytes are probably released singly into the sand. The spawning period was sharply defined, nearly all the worms spawning between 16 and 18 April 1949, about 3–5 days after full moon, when the highest tides occur at Chalkwell. There was a sharp rise in temperature at this time, which may have stimulated spawning (Fig. 1). Unspawned females quickly resorbed their oocytes after this, and a week or two later they had lost the white appearance characteristic of the sexually mature worms.

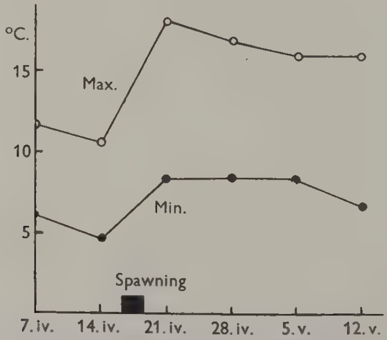

Fig. 1. Temperature of the natural habitat during spawning and early development. (Recorded by a max.–min. thermometer lying at a depth of 5 cm.)

There was little difference in size between the oocytes, either within a single female, or throughout the population. When ripe the oocytes are round, or slightly oval, and are surrounded by a fairly thick transparent layer which is adhesive at first, but which seems to lose this property when ready for spawning. They contain a large germinal vesicle, and a fine, opaque, granular cytoplasm (Fig. 2A).

The sperm plates are rather irregular in size and shape, and vary between 20 and 50 $\mu$ across. The sperm head is acorn-shaped, and bears a tail about 40 $\mu$ in length (Fig. 2B).

## Early Development of the Larvae

Development from artificial fertilizations, which were achieved by slitting open the adults and mixing the ripe gametes in a dish, proceeded only as far as late cleavage, and unfortunately no active larvae were obtained. Naturally spawned and fertilized eggs and cleavage stages were, however, collected from the sand.

A fertilization membrane was thrown off soon after artificial fertilization, and remained so close to the egg, that in many instances its presence was difficult to detect until the first cleavage. Polar bodies were conspicuous, and were thrown off about an hour after fertilization. The first cleavage, which takes place at right angles to the longitudinal axis of the egg, occurred after

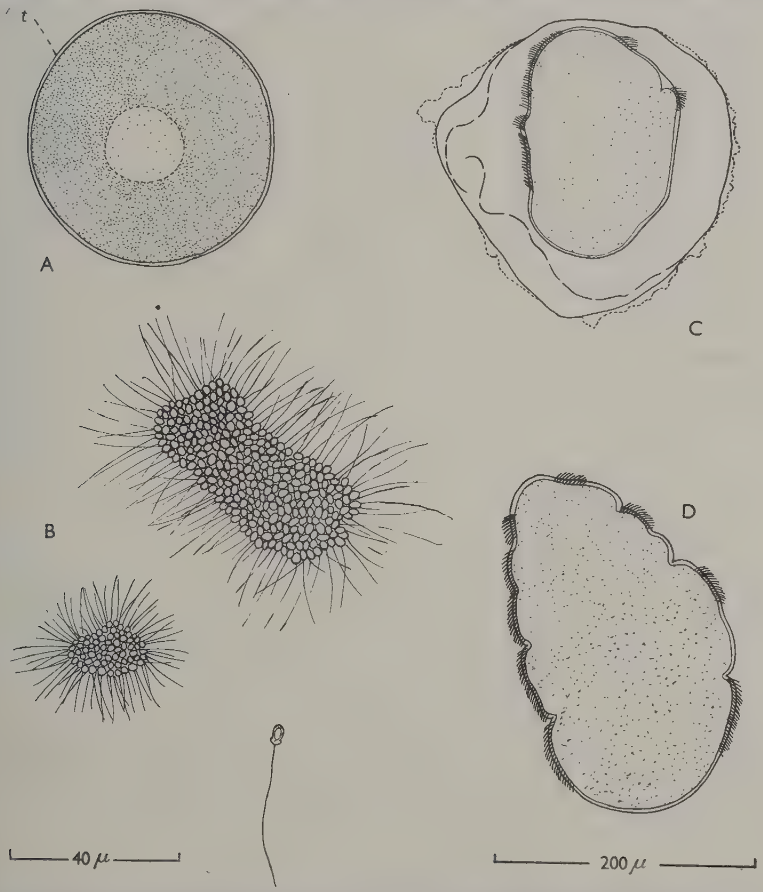

Fig. 2. Ripe coelomic gametes, and developmental stages obtained from the sand. A, unfertilized oocyte (*t*, transparent layer); B, sperm plates, and a motile spermatozoan; C, young unhatched larva; D, hatching stage. The scale on the left applies to B only; that on the right to A, C and D.

about 2 hr., the 4-cell stage being reached after about $3\frac{1}{2}$ hr., whilst 6 hr. after fertilization 8-cell stages may be seen.

In the natural habitat a jelly layer is very conspicuous, and stands away from the developing larva, and although in artificially produced larvae this layer was obviously present, it did not stand away from the surface of the egg as in those stages obtained from the sand. In nature, this layer forms a capsule in which the larva is free to rotate, and is practically opaque, owing to the rich growth of diatoms and other algae which it supports, so that in practice it is necessary to dissect off this capsule in order to see the larva. It may be added that the capsules can only be distinguished with difficulty from the surrounding sand grains which are much the same in size.

About 2 or 3 days after fertilization, cilia begin to grow out through the fertilization membrane, which then becomes the larval cuticle, and the larva begins to rotate within the egg capsule (Fig. 2C). The ciliation gradually extends down the ventral surface in a posterior direction, and well-marked bands of fine short cilia extend over the dorsal surface, the larva becoming more vigorous in its movements. Later, this ciliary movement is supplemented by muscular movement, the larva becoming highly contractile, but chaetae and other appendages are absent. Ten days after fertilization, the contractile movements are fairly vigorous and stretch the walls of the capsule, which eventually breaks open to release the larva. Late cleavage stages and gastrulae were collected from the sand on 19 April 1949, and on the 21st most of the larvae were rotating in their capsules, but no hatched larvae were found until the 28th, about 10 days after spawning.

On hatching, the larva is about 250 $\mu$ long, and has two to three segments delimited, but owing to the absence of chaetae, and to the extreme contractility of the body wall, it is difficult to determine the exact number of segments present. The larva is completely opaque, white, sausage-shaped, and with a slightly pointed anterior end. The ventral surface is uniformly ciliated, while bands of cilia extend round the dorsal surface in each segment (Fig. 2D), but the cilia are very short, and are insufficient to lift the larva off the bottom. Indeed, in spite of their well-marked muscular movements, the larvae are rather sluggish and are difficult to detect. Owing to the opacity of the body wall, no details of the gut or other internal structures could be seen.

## Discussion

The larva of this species is interesting in that it is typically bottom-living, non-pelagic, and lecithotrophic, as are the larvae of many other intertidal polychaetes, and has no pelagic stage, unlike any of the other cirratulid larvae known. Correlated with this habit are the relatively large oocytes and capsule in which the larva develops until two or three segments have been formed. The hatching larvae are similar to the early bottom stages of *Audouinia* *tentaculata*, described by Wilson, in the absence of chaetae, and in the extreme contractility of the body. Also, in the absence of chaetae, they resemble the corresponding stages of *Dodecaceria concharum*, figured by Mésnil and Caullery (1898). The larvae of *Audouinia tentaculata*, however, develop from much smaller eggs than those of *Tharyx marioni*, and the larvae of the former hatch in a relatively short time as ciliated planktonic trochophores. It is the metamorphosed bottom stages which may be compared with the hatching larvae of *T. marioni*, which develop from eggs one and a half times the size of those of *Audouinia tentaculata*. The development of *Tharyx marioni*, therefore, affords an interesting new example of the formation of a yolky egg and loss of an active pelagic stage.

## SUMMARY

Males and females of *T. marioni* occur at Chalkwell in equal numbers. The species is atoquous, the large oocytes being spawned into the sand where they are fertilized. Spawning took place over a sharply defined period (16–18 April 1949) following a sharp rise in temperature, and at a time when the highest monthly tides occurred. The larva hatches about 10 days after initiation of development. It is lecithotrophic, and at first achaetous and poorly ciliated, but very contractile. These two latter characters appear to be common to all cirratulid larvae known. There is no pelagic stage.

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# OBSERVATIONS ON THE STRUCTURE AND LIFE HISTORY OF *AUTOLYTUS PROLIFER* (O. F. MÜLLER)

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(Text-figs. 1–3)

## INTRODUCTION

All the specimens of *Autolytus prolifer* (O. F. Müller) described here were gathered from colonies of the hydroid *Obelia flabellata* Hincks, growing on pebbles in a shallow creek in the intertidal zone of the Chalkwell mud flats, on the north side of the Thames estuary. The syllid was found to be very plentiful on this hydroid, living in semi-transparent tubes attached to the stem, but was not found elsewhere.

The specimens agree well with previous descriptions of *Autolytus prolifer* in the number and arrangement of the pharyngeal teeth, and in the chaetae; but some of the other anatomical features show similarities with other species of *Autolytus* Grube.

Records of the occurrence of this species are scanty, due, no doubt, to lack of observation. Nevertheless, published descriptions have frequently been based on a few or even on single specimens, while here it may be pointed out that a relatively large number of worms of all ages were collected and examined.

In this paper the terms 'male form' and 'female form', or simply 'male' and 'female', have been used in place of the older terms, '*Polybostrichus*' and '*Sacconereis*' respectively.

The formation of stolons and the resulting female and male stages have been described by several previous authors (Slabber, 1778; O. F. Müller, 1788; Bruguière, 1791, table 56, figs. 8–15; Krohn, 1852; Max Müller, 1855; Keferstein, 1862; Greeff, 1866; St Joseph, 1887; McIntosh, 1908; Fauvel, 1923; de Vos, 1936; Thorson, 1946; Wesenberg-Lund, 1947), while a more general account is given by Potts (1911). Apart from de Vos, these authors appear to agree that, in the male form, only the first three segments behind the head are without natatory chaetae, whereas in the few males collected at Chalkwell six such undifferentiated segments separated the head from the metamorphosed segments. De Vos found the number of segments behind the head without natatory chaetae to be variable.

It is likely that the habit of living in tubes on hydroids is widespread among autolytoids. Wesenberg-Lund (1947) has found *Autolytus prolifer* on *Lafoëina maxima* Levinsen. McIntosh (1908) records *A. prolifer* from shells and other debris brought up by the deep-sea lines of fishermen at St Andrews (Scotland), and in tough translucent tubes under stones near low-water mark. These worms have also been found on seaweeds (McIntosh, 1908; Thorson, 1946).

The larval development of this species has not hitherto been described, though sketches of larvae attributed to *A. prolifer* are scattered through the literature. Some of these resemble the corresponding stages described here, but others are very different. Most of the work on autolytoid development has been done on other species, e.g. Agassiz (1863) on *A. cornutus*, and Malaquin (1893) on *A. edwardsi*.

The syllids were easily collected by gathering the *Obelia* colonies. On placing these in glass dishes, most of the worms deserted their tubes and aggregated on the side of the dish nearest the light, and were then easily removed with a small brush. Some of the youngest stages obtained, however, were collected later, for although these were not found to be living in tubes, they nevertheless adhered strongly to the surface of the perisarc.

Drawings have been made with the aid of a camera lucida, and with the exception of Fig. 1 from narcotized specimens. Details were checked from material fixed in 2% formalin in sea water, after narcotizing with 8% magnesium sulphate, and mounting in benzyl alcohol or euparal, either unstained, or stained with borax carmine.

Collections were made on 1, 6 and 21 June 1949.

## Identity and Structure

The ordinary non-reproductive stages ('*animal surculare*') resemble *A. prolifer* (O. F. Müller) in the following features: (i) two pairs of eyes with lenses, and one pair of lateral eyespots; (ii) most (but not all) individuals with an S-shaped pharyngeal curvature; (iii) pharynx always provided with ten, equal, teeth; (iv) oblong proventriculus; (v) coloration; (vi) chaetae.

In some other characters, however, these specimens differed from the published descriptions and figures of *A. prolifer* (O.F.M.), and in some features resemble *A. auriantiacus* Clap. These differences are: (i) the median head tentacle is invariably longer than the two lateral tentacles, and may be twice as long; (ii) dorsal cirri much shorter; (iii) male form with three regions behind the head—first with six anterior segments without natatory chaetae, second with about eighteen segments with natatory chaetae, third with about six undifferentiated terminal segments; (iv) smaller size (non-reproductive form 3–7 mm., cf. Fauvel (1923), 5–15 mm.); (v) some specimens show a looped pharyngeal curvature.

Most previous authors agree that the male form has only three undifferentiated anterior segments lacking natatory chaetae (Keferstein, 1862; Malmgren 1867; Langerhans, 1879, 1880; St Joseph, 1887; McIntosh, 1908; Fauvel, 1923; Wesenberg-Lund, 1947), and that the segments bearing natatory chaetae extend to the pygidium, although St Joseph notes that the terminal chaetigerous segment has shorter natatory chaetae than the others. De Vos, however, found between three and six such anterior segments, followed by twenty to twenty-seven segments bearing natatory chaetae, and that the female also varied in a similar way. On the other hand, the sexual phases described by Wesenberg-Lund all have three such anterior segments, and although the non-reproductive stages are similar to the Chalkwell specimens, the male is different in some respects. Wesenberg-Lund does not mention eye-spots (as distinct from lensed eyes), and unfortunately makes no reference to the pharyngeal armature.

The stock differs little from the drawing by Thorson (1946), except in the longer prostomial tentacle, and the much shorter parapodial cirri, but does not bear a close resemblance to drawings made by earlier workers on autolytoids ascribed to this species (Keferstein, 1862; McIntosh, 1908). Stoloniferous forms were found with a single male stolon, and forms with up to four female stolons. A single free male form was found on the hydroid, but no ripe female stages were found unattached. A specimen with a single male stolon is shown in Fig. 1 A, and a dorsal view of one of the parapodia from the differentiated region in Fig. 1 B. The dorsal cirrus will be seen to be much shorter than those figured by all previous authors. As well as showing the more obvious differences already described, Keferstein's male does not show a pair of anal cirri, which are clearly visible in the Chalkwell worms.

If these Chalkwell specimens are regarded as belonging to a new species, then they can only definitely be separated from *A. prolifer* (O.F.M.) by the sexual phase, unless the much shorter length of the dorsal cirri is regarded as a constant feature of taxonomic importance. This cannot be decided until the real affinities of the males with only three anterior segments without natatory chaetae ascribed to *A. prolifer* has been proved, but from the observations of de Vos (1936) it would appear that the number of segments behind the head without natatory chaetae is variable, and cannot therefore be regarded of taxonomic importance. This applies equally well to other species.

If, on the other hand, these worms are regarded as belonging to *A. prolifer*, then the pharyngeal armature alone supplies reliable separation from closely allied species such as *A. auriantiacus* Clap. It may be added that the teeth are difficult to see in *A. prolifer*, even in fixed and cleared material, and Johnston (1845, p. 146, pl. IX, figs. 3, 4; 1865, p. 192, pl. XV*a*, figs. 3, 4) thought that there were no teeth.

Other characters are variable, especially the length of the median head tentacle (Figs. 1, 3D–F). Claparède (1868), McIntosh (1908), and Fauvel (1923) all show the median tentacle to be the same length as the lateral tentacles, as in *A. brachycephalus* Mar. (Marenzeller, 1874), but Viguier (1886, p. 429, pl. XXVI, figs. 13–15; pl. XXVII, fig. 1) shows the median tentacle as being slightly longer, but not as long as in the specimens described here.

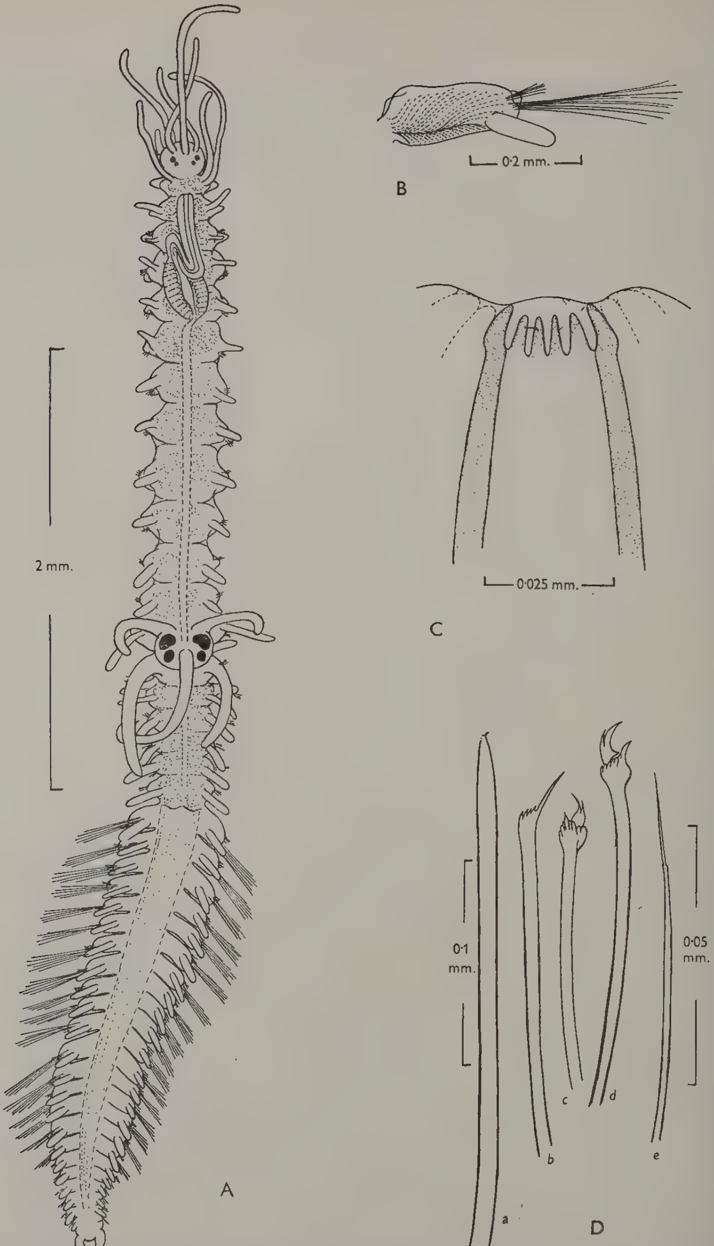
0·2 mm.
B
0·025 mm.
C
2 mm.
A
0·1 mm.
0·05 mm.
a
b
c
d
e
D

Fig. 1. *Autolytus prolifer*. A, stock with a single male stolon (dorsal view); B, dorsal view of a right parapodium from the differentiated region of the male form; C, pharyngeal armature; D, chaetae. *a*, distal half of a natatory chaeta from a male; *b*–*e*, chaetae from non-reproduction phase.

The looping and coiling of the pharynx has also been regarded as a character of taxonomic importance, but in several dozen adults examined at random for this feature, it was found to be variable. Fauvel (1923) states that *A. prolifer* has an S-shaped pharynx, while that of *A. auriantiacus* is completely coiled. In the Chalkwell worms, the length of the pharynx varied, and consequently although an S-shaped loop was usually formed when the proboscis was retracted, several specimens showed a complete coil as in *A. auriantiacus* (Fauvel, 1923, p. 313, fig. 120*a*; Marenzeller, 1874, Taf. VI, fig. 1), and it may be noted that *A. auriantiacus* itself is variable, since Claparède (1868) gives a drawing with a pharynx showing a double coil (pl. 15, fig. 1). In Chalkwell worms, also, the proventriculus was situated more anteriorly than segments 7–9, but this may be correlated with the somewhat smaller size of the adults (about 5 mm., see Fig. 3F).

Representative chaetae are shown in Fig. 1D. They resemble chaetae previously figured for *A. prolifer*, but many of these drawings might equally well be attributed to other species, so that no really significant conclusions may be drawn from this character. Fauvel states (1923, p. 312), that the capillary chaetae (Fig. 1D, *e*, in this paper), occur singly in all segments posterior to the third chaetigerous segment, but in the Chalkwell worms they were found to occur singly in every parapodium in larvae and young worms, but were often missing from older individuals. The type shown in Fig. 1D, *b* was never found in young stages, but was fairly common in older worms, and in the ventral bundles of the parapodia in the males.

McIntosh (1908) gives the rather lengthy synonomy of *A. prolifer*, but in the light of the present work it is doubtful how many of the descriptions do, in fact, refer to this species.

## REPRODUCTION AND DEVELOPMENT

The pelagic female of *A. prolifer* has already been described and figured by previous authors (Slabber, 1778; Krohn, 1852, 1855; Max Müller, 1855; Malaquin, 1890, 1893; McIntosh, 1908; Fauvel, 1923; Thorson, 1946).

There seems to be no fixed breeding season (Jensen, Johansen & Levinsen, 1904, pp. 286, 296; McIntosh, 1908, 1927; Allen, 1915; Thorson, 1946), although a spawning maximum probably occurs in late spring and early summer, as many of the records of the occurrence of specimens in the plankton refer to the period between April and July. At Chalkwell, stoloniferous forms, pelagic forms, and larvae were all found during June.

A few descriptions and figures of the larvae ascribed to *A. prolifer* are also scattered through the literature. Max Müller (1855) figures larvae from the egg-sac, and gives the size of the ripe egg as 50 $\mu$, and a young achaetous larva with two segments as about 200 $\mu$ in length. McIntosh (1908) gives a figure of a larva which could refer to almost any syllid, and his later drawings (1927) do not in the least resemble the larvae described here. Okada (1929), however, figures a larva rather more than 100 $\mu$ long, only slightly less advanced than the youngest stage found at Chalkwell, and although the smallest stage found here was about 300 $\mu$ in length, it showed only one more segment delimited. Okada's general remarks on the structure of syllid larvae apply to these larvae of *A. prolifer*.

It may be concluded that the eggs are small (100 $\mu$ or less in diameter) and develop into young achaetous larvae while still in the egg-sac suspended from the ventral surface of the female. Their pelagic life is probably not very long, and although they appear to undergo no great morphological differentiation during this period, they increase greatly in size and may treble their length. Martinus Slabber (1778) figures larvae emerging from the egg-sac of a female, and these larvae are already composed of head, pygidium, and two achaetous segments, and correspond with the youngest stage described here. On settling, they are still achaetous, and are about 300 $\mu$ in length (Fig. 3A). The body consists of a head region formed from a prostomium bearing an akrotroch anterior to two red eye spots, and a prominent prototroch posteriorly, which apparently corresponds to the buccal segment containing the pharynx. Okada (1929) could not distinguish these two parts of the head (prostomium and buccal segment), but they were clearly visible in the Chalkwell larvae. The pharynx lies entirely within the buccal segment, and does not project backwards into the peristomial segment which remains achaetous throughout life, and at this stage bears a prominent ciliary band (Okada's 'interparatroch'). The peristomial segment is followed by the future first chaetigerous segment, in which the chaetae may be seen developing internally (Fig. 2C), and which also bears a ciliary band. A further, relatively undifferentiated segment may be seen between this and the pygidium. A telotroch is not present, and does not develop until later, but the whole of the ventral surface is clothed with short cilia. Before the chaetae have been erupted from the first chaetigerous segment, two pairs of eyespots have been formed (Fig. 3), and a third pair, the most lateral in position, which remain without lenses, are added when three or four chaetigerous segments have been formed.

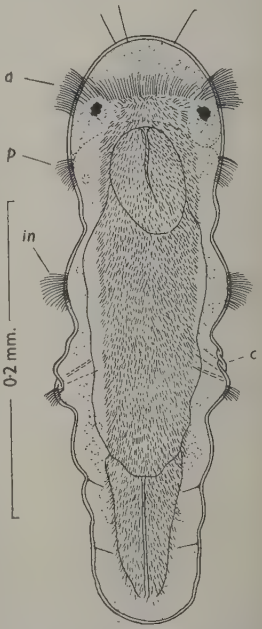

Fig. 2. *Autolytus prolifer*, young achaetous larva (ventral view) *a*, akrotroch; *in*, interparatroch; *p*, prototroch; *c*, first chaetigerous segment (chaetae not yet erupted).

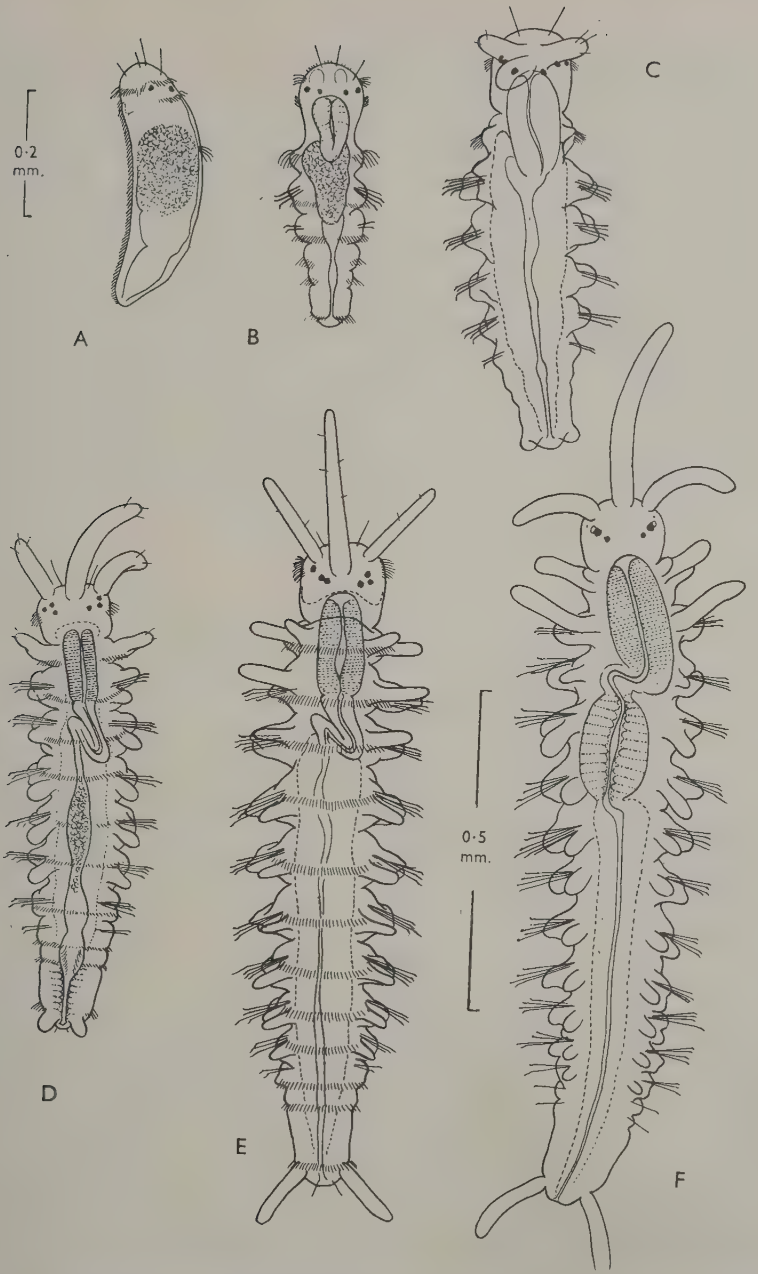

Fig. 3. *Autolytus prolifer*. A, a slightly later stage than in Fig. 2, seen in side view, showing two pairs of eyespots, and the ventral ciliation; B, larva with two chaetigerous segments (dorsal view); C, larva with five chaetigerous segments (dorsal view); D, young *Autolytus* with seven chaetigerous segments (dorsal view); E, a slightly older stage with nine chaetigerous segments (dorsal view); F, young *Autolytus* with thirteen chaetigerous segments, showing the proventriculus (dorsal view).

After the eruption of the chaetae from the first chaetigerous segment, further segments are added posteriorly, each segment bearing a ciliary band. A telotroch becomes clearly visible by the time two chaetigerous segments have been formed, but the ciliary band on the peristomial segment remains the most prominent tract throughout development. The ciliation is summarized in Table 1.

In larvae with two chaetigerous segments (Fig. 3B), the prostomial tentacles may be recognized. As will be seen from Fig. 3B–F, the prostomial tentacles gradually lengthen, while the dorsal cirri and the supplementary tentacles from the peristomium and the first chaetigerous segment gradually lengthen out rather later in development.

The gut remains in much the same condition for some time, but the pharynx, which at first is confined to the buccal segment, extends backwards. In larvae with two chaetigerous segments it extends into the achaetous peristomial segment, and, in larvae with five chaetigerous segments, into the first chaetigerous segment. The proventriculus is not formed until ten or eleven segments have been delimited, by which time the young *Autolytus* is over 1 mm. in length.

## TABLE I

CILIATION OF LARVAL *AUTOLYTUS PROLIFER*

| | | |
|---|---|---|
| Head | Prostomium | Akrotroch |
| | Buccal segment | Prototroch |
| | Peristomium | Interparatroch |
| | First chaetigerous segment | Ciliary band |
| | Second chaetigerous segment | Ciliary band |
| | Pygidium | Telotroch |

Larval chaetae do not appear to differ appreciably from those of the adult. At first, all the chaetigerous segments may contain a chaeta of the type shown in Fig. 1D, *e*, but these are not always present, and are often, apparently, lost. Most of the chaetae resemble those shown in Fig. 1D, *c*, *d*, but those similar to Fig. 1D, *b* were never seen in young larvae, and appear to arise later in development.

## SUMMARY

The mode of life and larval development of *Autolytus prolifer* (O. F. Müller) is described. The development does not appear to differ markedly from that described for other *Autolytus* species, although the larvae which have been described here are noticeably different from those of other species. In the present state of knowledge a detailed comparison is impossible. Most of the work done on these worms was performed about 50 to 100 years ago, and it is therefore interesting to note the general confirmation of the views of Okada on the constitution of larval syllids.

It seems likely that most of the life cycle is normally passed on a hydroid —in the locality investigated on a species of *Obelia*. There is probably no specific relationship, since these worms have been found on seaweeds and other objects.

Mucous glands are well developed, and the young larvae adhere strongly to the perisarc of the hydroid, even when unprotected by a tube. These tubes, which ramble amongst the branches of the host colony, are semi-transparent, straw coloured, and unbranched, and may be inhabited by several animals. During the winter when the hydroids die back, the worms presumably hide under stones or migrate to deeper water.

In the adults, anatomical features such as the form of the pharynx, position of the proventriculus, the relative lengths of the prostomial tentacles, and the number of segments in the male without natatory chaetae, all usually considered of taxonomic importance, have been found to be variable. Apart from the coloration, which is lost on preservation in alcohol, the number of the pharyngeal teeth alone distinguishes the species from *A. auriantiacus* Clap.

The male form collected from Chalkwell has six segments without natatory chaetae, behind the head. It is likely that the number varies between three and six.

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# ON *GAMMARUS ZADDACHI OCEANICUS* SEGERSTRÅLE

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(Text-figs. 1–3)

In a survey of the British species of *Gammarus* inhabiting estuarine waters (Spooner, 1947), it was found necessary to divide *G. zaddachi* Sexton into two well-marked morphological forms, with different salinity optima, which in fact behave as distinct species. They were, however, on account of their similarity in important structural features, retained as a single species and named *G. z. zaddachi* and *G. z. salinus* respectively. At the time little could be said about a third subspecies, essentially marine in its distribution (but ranging into brackish water), which Segerstråle (1947) independently described as *G. z. oceanicus*.

It is now clear that *G. z. oceanicus* is, geographically, the most widespread and abundant form of the three, occurring generally on shores in shallow coastal waters all over the boreal and subarctic region of the Atlantic area, southward to Britain, Denmark and the Baltic, and eastward along the Siberian coast at least to 140° E. On the American coast it extends southward at least to New York.

*G. z. zaddachi* and *G. z. salinus* are both temperate forms, and, as far as is known, confined to the brackish waters of Europe. In the Baltic Sea all three subspecies overlap very widely.

In this further contribution on *G. z. oceanicus* various records of occurrence are given which help to fill in the picture already outlined by Segerstråle (1947, 1948), but which in particular establish the existence of this form as dominant along much of the coast of Scotland.

The ecological relations existing between *G. z. oceanicus* and *G. locusta* on the one hand, and between it and *G. z. salinus* on the other, can now be discussed, but important gaps in knowledge still exist.

A fortunate chance of further exploring the *Gammarus* fauna of the more inaccessible parts of the north-western British coasts was provided by Dr Dorothy C. Gibb, who, in 1948 and 1949, collected a long series of samples of the fauna associated with the brown alga *Ascophyllum nodosum* var. *mackaii*. The great bulk of this fauna was found to consist of littoral gammarids. Among these, especially in the more northern stations, *Gammarus zaddachi oceanicus* occurred with some regularity, evidently flourishing in the littoral zone where this weed, amongst others, provides cover. I am much indebted to Dr Gibb for the opportunity of identifying the gammarids she had collected. The value of her samples is enhanced by the detailed information of the habitats she acquired during her investigations and will publish in due course.

To various zoologists whose help I have gratefully acknowledged in presenting or lending material of *G. zaddachi*, I must now add the following: Mr J. S. Colman, Mr G. R. Forster, Mr N. A. Holme, and Dr Sven Segerstråle. It has been very instructive to compare samples of different forms from the Baltic, sent to me by Dr Segerstråle, with our own.

My special thanks are also due to Dr Isabella Gordon for the facilities afforded to me for examining the material preserved in the British Museum.

## THE CHARACTERS OF *GAMMARUS ZADDACHI OCEANICUS*

A description is given by Segerstråle (1947, pp. 226–9, fig. 3, *a–g*). The main *zaddachi* characters are seen in the form of the gnathopods (in each sex), the well-excavated lateral sinus of the head, the moderate depth of the coxal plates, the shallow rounded ventral expansion of coxal plate 4, the moderately produced epimeral plates, and in the somewhat shortened uropod 3 inner ramus. The arrangement of the antennal hair tufts is also really typical of the species, although the relative shortness and sparseness of the hairs renders this feature much less obvious.

The hinder part of the body is relatively glabrous, as in *G. z. salinus*. Younger specimens of the two subspecies resemble each other closely, but can be distinguished at least by reference to the characters of antenna 1. Adults are readily told apart by the setation and structure of antenna 1; by the dorsal profile of the urosome; and, in life, by the body coloration (see below). From *G. z. zaddachi*, it is further distinguished by the lack of those features in which this relatively hairy form differs from *G. z. salinus* (see Spooner, 1947, pp. 20–1). *G. z. oceanicus* also reaches considerably larger sizes than either of the other two forms, even near the southern limit of its geographical range.

*Antenna* 1 (Fig. 1). The peduncle of this limb provides the most critical diagnostic feature of *oceanicus*, approaching, as it does, that of *G. locusta*. The hair tufts on the ventral surface are sparse: on segment 1 there are two thin tufts (excluding the apical tuft), rarely a small third, composed of very few shortish hairs, as contrasted with at least four tufts in *G. z. salinus*, and one tuft (sometimes a second slight one) in *G. locusta*; on segment 2 there are normally three tufts, as compared with at least four in *G. z. salinus* and one or two in *G. locusta*; on segment 3 there is one strong tuft, which is often entirely lacking in *G. locusta*, and represented by at least two tufts in other *G. zaddachi*. The relative lengths of the segments approximate to ratio of 10:7·4:3·4, that is to say segments 2+3 are together a little longer than segment 1 (much longer in other *zaddachi*, and just shorter in *locusta*).

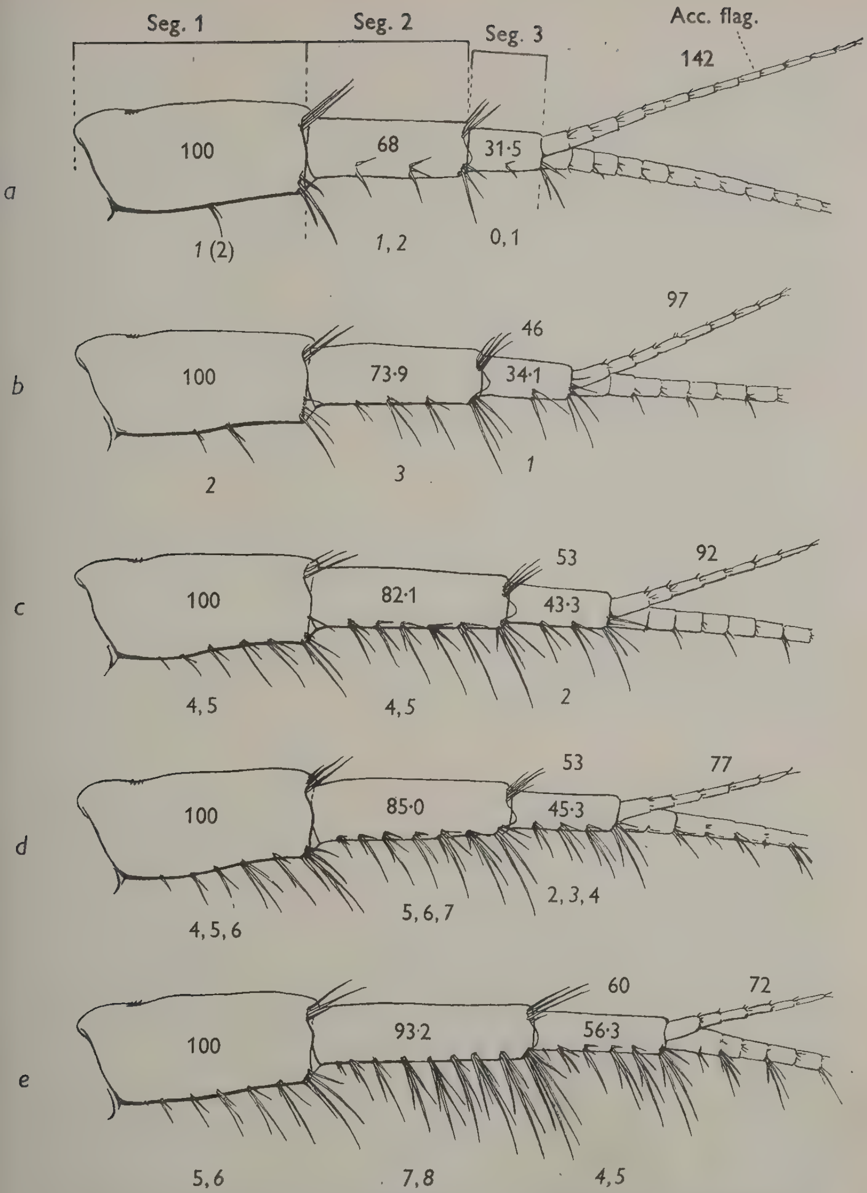
Seg. 1
Seg. 2
Seg. 3
Acc. flag.
142
a
100
68
31·5
1 (2)
1, 2
0, 1
97
46
b
100
73·9
34·1
2
3
1
53
92
c
100
82·1
43·3
4, 5
4, 5
2
53
77
d
100
85·0
45·3
2, 3, 4
5, 6, 7
4, 5, 6
60
72
e
100
93·2
56·3
5, 6
7, 8
4, 5

Fig. 1. Antenna 1 peduncle of an adult male of (*a*) *G. locusta*, (*b*) *G. zaddachi oceanicus*, (*c*) *G. z. salinus*, (*d* and *e*) *G. z. zaddachi*; drawn somewhat schematically, viewed from the inner surface. The numbers written on the segments and against the accessory flagellum refer to the mean length relative to the first segment as 100. The end-points of measurements are indicated at the top of the diagram (against the peduncle segments of *a*). The number written above segment 3 refers to the ratio of this segment to segment 2. The numbers written below the segments represent the typical number of ventral hair tufts present in adults of various ages; those italicized being the most characteristic.

Segment 3 is just less than half segment 2 (as in *locusta*), whereas it is a little longer than half segment 2 in other *zaddachi*. The ratios given in Fig. 1 represent typical proportions and have been calculated from the averages of several accurately measured limbs from adult males. Further reference to this diagram will show a distinct gradation of various metrical characters with *G. locusta* at the end of the series and the most intensely hairy *G. z. zaddachi* at the other. The condition in *G. z. oceanicus* is diagnostic, and is rather closer to *G. locusta* than to other *zaddachi*. The accessory flagellum length is somewhat longer in *oceanicus* than in *salinus*, possessing 9 or 10 segments in the larger males, but well short of the unusual length of this limb in typical *G. locusta*.

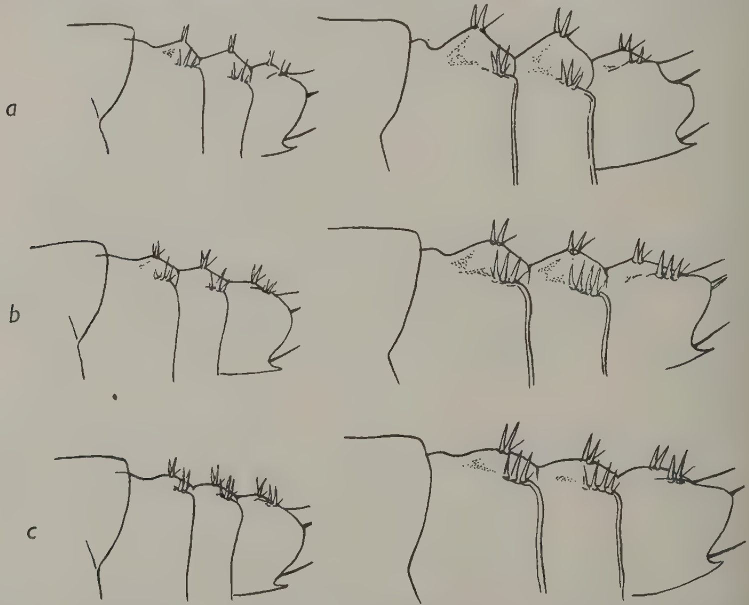

Fig. 2. Dorsal part of urosome viewed laterally, of (*a*) *G. locusta*, (*b*) *G. zaddachi oceanicus*, and (*c*) *G. z. salinus*; immature animal on left, adult male on right.

*Urosome*. In the degree of elevation mid-dorsally of urosome segments 1 and 2, *G. z. oceanicus* is intermediate between *G. locusta* and *G. z. salinus* (Fig. 2). The elevations are distinctly angled, but make an angle of some 135°, whereas in a comparable stage of *G. locusta* they are nearly right-angled. The elevations of *G. z. salinus* are distinctly flattened.

*Body colour*. This is of a variety of shades of brown (reddish olive to greenish or yellowish), often semi-transparent, without strong banding, at most a suffused darkening along the margins of the segments. The female is usually darker (as in *G. locusta* and *G. z. salinus*). Lateral orange pigment patches may be present on pleon segments 1–3, but these may be lacking or composed of colourless globules. (In Finland, it seems they are usually lacking or at least colourless.) There are never spots on the mesosome segments laterally, as in *G. locusta*. Where *G. z. oceanicus* and *G. z. salinus* occur together, it is apparently possible to separate the latter by eye owing to its stronger transverse banding.

*Size.* Adult males normally appear to reach a length of 22–25 mm. (from rostrum to apex of telson) in Scotland, the maximum observed being 27·5 mm. Segerstråle gives maximum of 26 mm. for the Baltic, and Stephensen (1940*a*,*b*) one of 38 mm. for the Arctic, and a single exceptional male of 39 mm. from Iceland. The eggs are of similar proportions to those of other *zaddachi*.

*Habitat.* Being a marine coastal form, inhabiting the algal zone of shallow waters up to the mid-tide level of the shore, it is apt to occur in company with *G. locusta* in the more southern part of its range (see p. 138). No difference in the general habits of the two forms is yet known. Being also tolerant of some degree of dilution of the sea water and thus penetrating into estuaries, it reaches the zone inhabited by *G. z. salinus*, in so far as the geographical ranges overlap (see p. 137). Apart from these two, it will not normally be accompanied by any other *Gammarus* (s.s.) species in samples from the British Isles. Exceptions to this rule may be found in certain 'mixed' habitats, e.g. at coastal outflows of fresh water which permit the fauna of a stream to mix with that of the shore over which it flows.

## Distribution of *GAMMARUS ZADDACHI OCEANICUS* in Britain

A full list of the British localities from which *G. z. oceanicus* has been recognized is now given. The specimens in question have all been examined by the writer. The following abbreviations are used: G, from the collections of Dr Dorothy Gibb, all from the middle of the intertidal zone amongst *Ascophyllum*. A.D.H., Prof. A. D. Hobson; B.M., British Museum; coll., collected by; Coll., collection. Localities are classified under vice-counties according to the customary scheme (see, for example, Roebuck, 1921).

**Scotland.** W. Sutherland. Loch Laxford, N. side, Loch a Chadhfi, G, 22. ix. 48, 5 ♂♂, 6 juv. (apparent inhibited development); Weaver's Bay, G, 21. ix. 48, bays on east and west side, 1 ♂, 3 ♂♂. Badcall Bay, N. side, G, 21. ix. 48, 2 juv. Kylestrome, G, 20. ix. 48, 2 small ♂♂, 1 juv. W. Ross. Gairloch, Badachro Bay, G, 17. v. 48, 1 young ♂. Loch Torridon, Camas Roil, G, 15. v. 48, 5 ♂♂, 5 ♀♀; Ob Mheallaidh, 8. v. 48, 5 ♂♂, 6 ♀♀. Loch Long, Conchra, G, 18. v. 48, 3 ♂♂, 2 ♀♀. Loch Duich, G, in four sites at which samples were taken regularly: site 1, in company with *Gammarus duebeni* (fresh-water seepage over shore), between 18. vi. 48 and 19. i. 49, 21 ♂♂, 8 ♀♀, 1 juv.; site 2, between 18. vi. 48 and 31. v. 49, 29 ♂♂, 10 ♀♀, 3 juv.; site 3, between 18. vi. 48 and 3. iii. 49, 19 ♂♂, 10 ♀♀, 7 juv.; site 4, between 18. vi. 48 and 31. v. 49, 41 ♂♂, 18 ♀♀, and 4 juv. N. EBUDES. S. Rona, vii and viii. 37, A.D.H. Coll., in stream flowing over shore, well below H.W., ♂ and immature (Beadle & Cragg, 1940, as '*zaddachi* hairless var.'; Spooner, 1947, p. 43). Raasay, vii and viii. 37, A.D.H. Coll., in stream over shore, 6 ♂♂, 1 ♀, 11 immature (Spooner, 1947, p. 43). Skye: Loch Dunvegan, G, 2. iv. 48, 2 ♂♂, 2 ♀♀; Loch Eishort, G, 6. iv. 48, large ♂ and ♀; Loch Ainort, G, single examples on two occasions (28. x. 48 and 16. xii. 48) at one of four sites regularly sampled between vi. 48 and vi. 49; Strollamus, G, at site 3 (one of three sites regularly sampled), on six dates between 26. iii. 48 and 8. vi. 49, 8 ♂♂ and 9 ♀♀. WESTERNESS. Loch Nan Cilltean (stream inflow), G, 8. iv. 48, ♂ and 2 ♀♀, in company with both *G. z. salinus* and *G. z. zaddachi*. MID EBUDES. Mull: Loch Selve, G, 12. iv. 48, in two samples, 15 ♂♂, 10 ♀♀. ARGYLL. Loch Sunart, G, 9. iv. 48, 7 ♂♂, 4 ♀♀. Loch Feochan, G, 1. iii. 48, 11 ♂♂, 7 ♀♀. Loch Riddon, G, in two of three sites regularly sampled, a few examples only—site 1, 1. ii. 49, 1 ♂, 1 ♀; site 3, 11. xi. 48, 1 ♂, 21. xii. 48, 1 ♂, 1 intersex, 1 ♀, 1. ii. 49, 1 large ♂. CLYDE ISLES. Cumbrae, east of Keppel Pier, shore near L.W., 16. ii. 43, 2 large ♂♂ (Spooner, 1947, p. 42 as *salinus*; specimens recently re-examined). No further examples have yet been obtained in the Millport area, where *G. locusta* is undoubtedly the commoner form. KINCARDINE. Muchalls, vii. 49, G. R. Forster, 22 ex. among sample of gammarids collected on the shore, including 8 mature ♂♂, 1 large ♀, and 13 young adults and immatures. FORFAR. Firth of Tay, among the Tees Survey collections (Alexander, Southgate & Bassindale, 1935), in sections IX and X of the estuary (Spooner, 1947, p. 43, as Segerstråle's subspecies = *oceanicus*; p. 52, as '*G. zaddachi* saline form'.)

**England and Wales.** DURHAM. Ryhope, Norman Coll. as '*locusta*' (B.M. 1911. 11. 8. 18866–70, part), 2 ♂♂, 2 ♀♀ ovig., 1 imm., with 3 *G. locusta*. N.E. YORKS. Robin Hood's Bay, one juvenile, shore between Mill Beck and Stoupe Beck, J. S. Colman and F. Segrove (who inform me that *G. locusta* is the common marine species here, as I was able to see for myself in October 1950).

The distribution map (Fig. 3) gives a fair impression of the extent of the range of *oceanicus* in Britain. There is reasonable negative data for localities south of the areas mentioned, that on the east coast being weakest. Dr Gibb's material includes ten samples from the north and west coasts of Ireland, collected under similar conditions to those from Scotland. *G. z. oceanicus* is lacking in these as well as in such other Irish material as I have seen. The Isle of Man, too, seems to be beyond the southern limit: Mr N. S. Jones (*in litt.*) has kindly confirmed that *oceanicus* has not yet been recognized there. Robin Hood's Bay would seem to be close to the extreme southern limit on the north-east coast, as is Heligoland on the other side of the North Sea.

## DISTRIBUTION ABROAD

The essential northern character of the range of *G. zaddachi oceanicus* was shown by Segerstråle (1947, fig. 4). Additional localities in north-east Europe were given by Segerstråle in 1948; and others identified by the present writer, hitherto unpublished, are listed in Appendix I (p. 142).

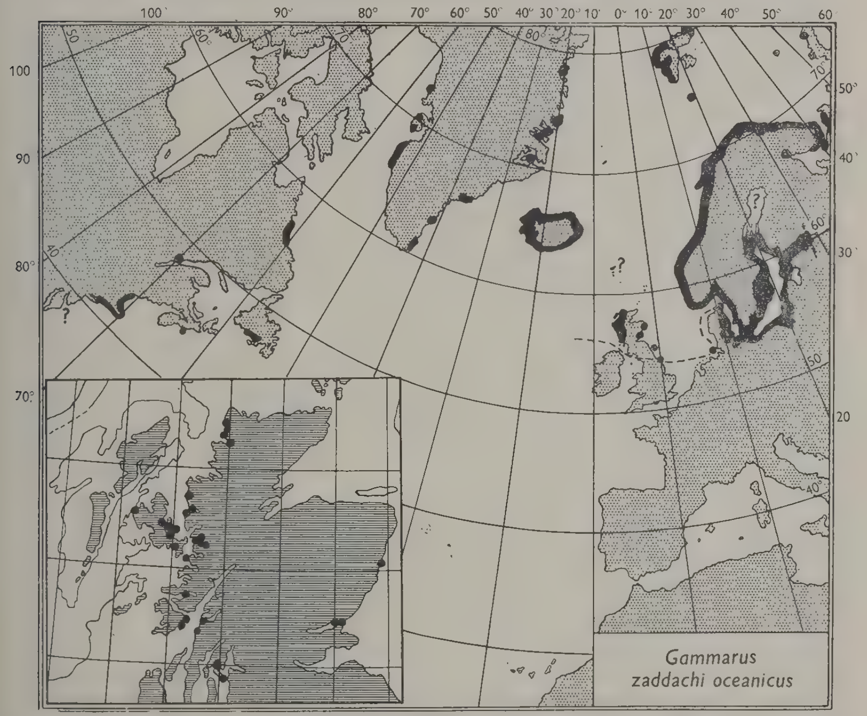

Fig. 3. Distribution of *G. zaddachi oceanicus*, showing regions in which it has so far been identified, except for its eastward extension to 140° E. along the north coast of U.S.S.R. Inset, localities from which *G. z. oceanicus* has been identified in Scotland. *Note.* The exact locations of Labrador and Newfoundland samples are not known. The absence of records along much of the east coast of Scotland is simply due to lack of investigation.

It is now possible to take account of the records given by Stephensen (1940*a*, *b*, 1944), Holmes (1904), Dementieva (1931), and Gurjanova (1929, 1931, 1932, 1936), records which can, for some good reason or another, be attributed with certainty to *G. zaddachi oceanicus*. These authors have given much information on the status of *Gammarus* in northern waters, and in the light of present knowledge it is often possible to distinguish clearly which of their observations refer respectively to *G. wilkitzkii*, *G. setosus*, or *G. zaddachi oceanicus*. All necessary details are given in Appendix II (pp. 144–7).

The more complete picture now obtained of the geographic range, though still incomplete with regard to its extreme eastern and western limits, may be summarized as follows (Fig. 3).

Coasts bordering the Arctic Ocean southward from the south fringe of Franz Joseph Land (60° E.) and north-east Spitsbergen, both areas lying on the 80th parallel. North coast of Siberia, from at least 140° E. (Brothers Laptev Sea) westward. Novaya Zemlya, at south-western end of the northern island, and west coast of the southern island. Spitsbergen, along the whole western side, where apparently the commonest gammarid. Bear Island. North coast of Russia, on the shore of the Kara Sea and of Chashskaya Bay, westward along the Kanin Peninsula and White Sea coasts. [No published data for coast between 67° and 48° E.] Murmansk coast generally, continuing along whole coast of Norway, southward to Oslo Fjord. Kattegat and all Baltic coasts south of 63° 30′ N. Heligoland. Great Britain, southward to coast of north-east Yorks and Firth of Clyde. (Faeroes?) Iceland, on north, east and west coasts. Greenland coasts to 77° N. on the east side and 73° N. on the west. North American Atlantic coasts including Labrador, Gulf of St Lawrence, Newfoundland, Nova Scotia, Massachusetts, and Connecticut, possibly extending farther south (see p. 140).

It occurs mainly in shallow coastal waters, captures in depths greater than 25 m. being mainly close to the shore, such as in the Norwegian fjords. There are, however, occasional records from deeper water in the open sea. In arctic and subarctic waters it is often accompanied by *G. setosus* Dement. (a species more exclusively restricted to the tidal zone and very shallow water) and sometimes by *G. wilkitzkii* Birula ( a species less restricted to the immediate vicinity of the shore).

The extent to which overlapping occurs with the temperate forms *G. locusta* and *G. zaddachi salinus* is discussed below (pp. 137–9).

On many northern shores *G. zaddachi oceanicus* is a dominant littoral animal, and must be of great account bionomically. For example, in Iceland, it is 'one of the most frequent littoral Amphipoda, occurring almost everywhere along the coasts of Iceland....On account of its enormous frequency it is of considerable importance as food for many valuable fishes, as young gadids and plaice, but especially for the charr, when living in saltwater.' (Stephensen, 1940*b*; as *G. locusta* (L.) s.s., p. 56.)

Its hardiness and adaptability are shown by its persistence in areas such as Cheshskaya Bay, east of the Kanin Peninsula, the restricted fauna of which is discussed by Gurjanova (1929); and more especially, along the north Siberian coast, on the shore of the Nordenskiöld Sea between the meridian 120 and 140° E. The sea here has greatly reduced salinity owing to the discharge of the Lena and other Siberian rivers, and the temperature is always below zero C. The fauna of the littoral is necessarily reduced, with a tidal range of only a few inches; and the adverse effects of ice action and lack of algal cover reduce it further. The only species of littoral animal recorded, indeed, was *G.* '*locusta*' (= *zaddachi oceanicus* + *setosus*) (Popov, 1932).

## RELATION TO *GAMMARUS ZADDACHI SALINUS*

*G. zaddachi salinus* does not tolerate normal sea-water salinities, and so, in Great Britain, it is virtually confined to estuaries. It is found, however, in marine habitats when the salinity does not rise above 31 ‰, as in part of the Bristol Channel. In the Baltic Segerstråle (1947) has found it to be widely spread.

In the Scottish records previously given (Spooner, 1947, p. 42), that for Cumbrae should be transferred to *oceanicus*, but the Fairlie Sands and Clachan Strand records apply to typical specimens of *salinus*. Additional British localities for *G. z. salinus* are given below, which establish its occurrence in Cumberland, in the west and north of Ireland, and well up on the west and east coasts of Scotland. (As before, G refers to Dr Gibb's material.)

**England and Wales.** S. DEVON. R. Yealm estuary, present in both Cofflete and Newton Creeks (in 1948), but confined in them to a stretch of a few hundred yards. R. Exe estuary, present in small sample of gammarids taken near Starcross, 23. vi. 47. GLAMORGAN. Cardiff, Bristol Channel off Flatholme, coll. R. D. Purchon, 12. ix. 47, 4 ♂♂; in trawl 29. ix. 47, ♂, 4 ♀♀ (conforming with occurrence on the opposite Somerset coast). CUMBERLAND. R. Esk estuary, at Eskmeals, 31. v. 50, plentiful in river channel, upstream from the railway bridge, in company with *G. z. zaddachi*. E. NORFOLK: Breydon, coll. R. Gurney, viii.–21, 1 ♂ (B.M. 1949.11.30.9.)

**Scotland.** ARGYLL. Loch Riddon, G, at two of three sites regularly sampled over a year: site 2, 11. viii. 48, 1 ♂ and 1 ♀; site 3, 30. ix. 48, 1 ♂, 2 ♀♀, 1 juv., 11. xi. 48, 3 ♂♂, 1. ii. 49, 1 ♂ (in site 3 accompanying *G. z. oceanicus*). WESTERNESS. Loch Nan Cilltean, G, 8. iv. 48, 3 (2 ♂♂ and 1 ♀ with eggs) in a sample containing also 3 *G. z. oceanicus*, 5 *G. z. zaddachi*, 7 *Marinogammarus marinus*, and 1 *M. stoerensis*, showing clear mingling of faunas of stream and shore. S. ABERDEEN. Aberdeen, coll. G. R. Forster, 1949, 2 ♂♂. N. ABERDEEN. Newburgh, estuary of R. Ythan, coll. G. R. Forster, vii. 49, 3 ♂♂, 1 ♀, 2 juv.

**Ireland.** W. DONEGAL. Mullroy Bay, G, area 1 (head of estuary), 8 ♂♂, 7 ♀♀ (breeding), in company with about equal number of *Gammarus z. zaddachi*. N. GALWAY. Ballynakill Bay, G, north-east corner, 4 juv. with 1 ♀ *G. z. zaddachi*.

There is therefore a region of considerable extent along the west coast of Scotland (at least from the Firth of Clyde to the border of West Ross (probably farther); as well as the greater part of the north-east coast of England and east coast of Scotland, where *oceanicus* and *salinus* may come in contact. The Tay estuary samples contain only *oceanicus* in the region where *salinus* would be expected, but the number of specimens is small, and no significance can be attached to the absence of the latter. More detailed investigation in this region would be of interest. That *oceanicus* and *salinus* can overlap, in the way that *locusta* and *salinus* overlap, is shown by the samples from Loch Riddon and Loch Nan Cilltean. In the last, unique so far for Britain, all three subspecies of *G. zaddachi* occur together, as frequently may happen in collections from parts of the Baltic.

There is no evidence at all of intergrading between *salinus* and *oceanicus*, and it may be inferred that, as has been proved between the typical form of *zaddachi* and *salinus*, they cannot interbreed. For all practical purposes, therefore, the three forms can be treated as distinct species.

## OVERLAP WITH *GAMMARUS LOCUSTA*

Speaking broadly the marine 'niche' occupied by *G. zaddachi oceanicus* in the north is occupied by *G. locusta* (L.) in south Britain and the Low Countries southward. There is therefore special interest attached to the question of the ecological relations of the two forms in those areas in which overlap occurs. So far an adequate detailed investigation has not been made, but would certainly be valuable.

In Europe the overlap zone begins in Denmark. *G. locusta* is still the dominant form on the west coast, where indeed the existence of *G. z. oceanicus* has still to be proved. On the Baltic shores both forms are numerous, and *oceanicus* becomes dominant passing eastwards into the low salinities of the Baltic Sea. As Segerstråle (1947) shows, *locusta* reaches Finland but has a lower limit of some 5·5 $^{\circ}/_{\circ\circ}$, while *oceanicus* persists to about the 2·5 $^{\circ}/_{\circ\circ}$ isohyaline. Along the whole coast of Norway *oceanicus* is clearly dominant, *locusta* occurring sparingly from Oslo fjord to 70½° N. (Appendix II, p. 146). In Iceland the occurrence of *locusta* has recently been proved (Segerstråle, 1950), but it is clearly overwhelmingly outnumbered by *oceanicus*. There is nothing in the data associated with these continental records to suggest any important difference in habitat, except only that *oceanicus* is rather more tolerant of reduction in salinity.

In Britain, passing northwards, all that can be said so far is that *locusta* is still the dominant form at the known southern limit of *oceanicus* (Clyde Sea Area and north-west Yorkshire), but in no great distance *oceanicus* becomes at least as frequent as *locusta*. At least this is so in the sheltered lochs of the west coast, where *oceanicus* perhaps adapts itself more readily to the variously lowered salinities. Among Dr Gibb's samples of the *Ascophyllum mackayi* fauna there were very few *locusta* at all. On the other hand, only *locusta* have so far been seen in samples from Muck (Inner Hebrides) and Barra (Outer Hebrides). There is a distinct tendency for samples to contain only one or other of the two forms, and some real segregation by habitat is suggested. It is this aspect, in particular, which requires further study.

## THE BREEDING PERIOD OF *GAMMARUS ZADDACHI OCEANICUS*

In Britain most species of *Gammarus* breed in all months of the year, including *G. zaddachi zaddachi* and *G. z. salinus*. Segerstråle (1950) finds that these two forms also breed throughout the year in Finland, but points out that *G. z. oceanicus* has a resting period from the end of July to mid-November, and that during August, September and October no females could be found with broods in their pouches.

Evidence from British samples also points to a non-breeding season in the autumn for *oceanicus*. Females which are not breeding have their brood-plates reduced to an immature condition (smaller in size and lacking the fringe of finger-like processes): they are therefore at once recognized from females which are potentially capable of breeding, even if the contents of the brood pouch have been discharged or accidentally lost after preservation.

TABLE I. BREEDING IN *GAMMARUS ZADDACHI OCEANICUS*

| | Adult females | | Approx. percentage breeding |
|---|---|---|---|
| Period | Developed | Undeveloped | |
| 1 Jan.–6 Feb. | 8 | 5 | 60 |
| 7 Feb.–14 Mar. | 18 | 1 | 95 |
| 15 Mar.–20 Apr. | 23 | 0 | 100 |
| 21 Apr.–26 May | 13 | 0 | |
| 27 May–2 July | 4 | 0 | |
| 3 July–7 Aug. | 3 | 2 | 60 |
| 8 Aug.–13 Sept. | 1 | 3 | 25 |
| 14 Sept.–19 Oct. | — | — | — |
| 20 Oct.–25 Nov. | 0 | 3 | 0 |
| 26 Nov.–31 Dec. | 3 | 14 | 20 |

Table I shows the results of analysing Dr Gibb's west-Scottish material. The year is divided into ten periods. In the first column is given the number of reproductively active females observed, and in the second that of females clearly large enough to be mature, but with reduced brood plates. The latest animal with a brood was taken on 11 September, and the earliest on 4 December. But there is evidently considerable variation among individuals, and the rest period for any single individual could easily be 5 months. The data, as far as they go, indicate a non-breeding season from early September to mid-December, with its peak at the end of October. There is maximum breeding in March, April, May and June.

The onset of the non-breeding season appears to be later than in Finland by perhaps a month or 6 weeks, and renewal of reproduction also to be later by about a month.

## *GAMMARUS ZADDACHI OCEANICUS* IN AMERICA

A few years ago, through the kindness of Mrs Sexton, I was able to examine some so-called *G. locusta* from eastern North America (lent by Dr C. R. Shoemaker). From sketches and measurements made at the time it was subsequently noted that the specimens belonged not to *locusta* s.s., but to *zaddachi oceanicus*. The data attached to the specimens were 'Newfoundland, 1885'.

The same belated conclusion is also true of a sample of 6♂♂ (largest 31 mm.) from 'Lac Tadoussac: July 1938: V.D.V.', lent to me in 1939 by Mr G. I. Crawford. This locality is on the Gulf of St Lawrence.

Segerstråle (1947, p. 230) has indeed drawn attention to the occurrence of *G. zaddachi oceanicus* on the Atlantic coast of North America, having identified one sample from Labrador and two from Massachusetts. These would previously have been regarded as '*locusta*'.

More recently four additional samples of N. American '*locusta*', from Nova Scotia, and the New England states (see Appendix, p. 144, for details), have been critically examined and found to be *G. zaddachi oceanicus*. These are in the British Museum Collection. All date from about 1880, and had originally been determined as *G. ornatus* Edw. on S. I. Smith's authority.

The question arises whether the true *G. locusta*, as we now undertand that species (Sexton, 1942; Spooner, 1947), occurs on the western side of the Atlantic at all. A search for clues amongst the American literature has provided a fairly certain answer: the common species which for long has passed under the name of *locusta*, and earlier on of *ornatus*, is in fact *G. zaddachi oceanicus*.

In his work on the Amphipoda of southern New England, Holmes (1904, pp. 500–1; pl. X, no. 3) gives a description, some illustrations, and a photograph of the *Gammarus* '*locusta*' of that region (syn. *G. ornatus* Edw.), describing it as 'the species of amphipod decidedly most often met with in the collections from New England'. This cannot possibly be the true *G. locusta*, as is at once apparent from the photograph on his plate X (no. 3). In this the relative depth of the coxal plates, the shape of coxal plate 4, the depth of the lateral head sinus, the relative length of antenna 1 peduncle segment 2 and of the accessory flagellum, etc., are characteristic of *G. zaddachi oceanicus* as opposed to *G. locusta*. Furthermore, the drawings of the male gnathopod 3 and uropod 3 (figure on p. 501) show diagnostic features which exclude *G. locusta* and conform to *G. z. oceanicus*. Other points in the written description again agree with the latter against the former (accessory flagellum of 8 segments; the spination of male gnathopod 2 hand; no orange pigments on mesome); and there is no hint that a mixed population is being described.

There is thus as yet no evidence that *G. locusta* (L.) occurs on the American side of the Atlantic, and until positive evidence is forthcoming it can only be assumed that all references to *G.* '*locusta*' on the Atlantic seaboard refer to *G. zaddachi oceanicus*. The validity of the name '*ornatus*' will have to be seriously considered.[1]

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[1] Milne-Edward's (1830) description referred to specimens from Boston, Mass. It is sufficiently detailed to exclude all species except *G. zaddachi oceanicus* and *G. locusta* s.s., hence might be held to define the former by elimination.

(N.B. Statements referring to the occurrence of *G.* '*locusta*' on the Pacific coast of America should be heavily queried. South of the Behring Sea it is furthermore very doubtful whether records apply even to a related species.)

The extent to which *G. zaddachi oceanicus* ranges southward along the Atlantic shore of the U.S.A. is not known. As it is so plentiful on the Connecticut coast, it might well extend beyond New Jersey; but if its southern limit is reached as comparatively abruptly as in Britain, it may not exceed the 40th parallel of latitude.

Segerstråle (1947, fig. 3*f*) figures the telson of a specimen from Massachusetts, showing that two of the apical setae are delicately plumose. The first American male which I examined in detail also showed precisely the same feature but several others do not. Otherwise the possession of plumose setae (excepting the pleopods and uropod 3 rami) is a diagnostic feature of *G. setosus* Dement., in which all, or nearly all, the hairs on the urosome dorsally and on the telson are of this type.

## SUMMARY

A number of records of *Gammarus zaddachi oceanicus* from northern Britain are given, which indicate that this form extends down the respective coasts to the Clyde Sea Area and Yorkshire.

It is an important subarctic and boreal littoral crustacean which formerly was confused with *G. locusta*. Some additional localities are quoted and some re-identifications are made from literature, when illustrations or biometric data enable this to be done.

The ecological relations between *G. z. oceanicus*, on the one hand, and *G. z. salinus* and *G. locusta*, on the other, are discussed.

It is emphasized that the animal which has all along been known in eastern America as *G. locusta* (formerly *G. ornatus*) is really *G. z. oceanicus*.

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## APPENDIX I

### LIST OF SPECIMENS OF *GAMMARUS ZADDACHI OCEANICUS* EXAMINED (OTHER THAN BRITISH). NEW, OR REVISED, IDENTIFICATIONS

(G.I.C., G. I. Crawford. B.M., British Museum.
Cop.Mus., Copenhagen Museum)

**Baltic & Kattegat**

POMERANIA. Strela-Sund, near Stahlbrode, E. of Stralsund, Dr E. Schwarz, as *G. locusta*, 16 ♂♂, 3 ♀♀ (ovig.), with 2 *G. z. salinus* (B.M. 1933.

11. 1. 2–10, part). S.W. SWEDEN. Bohuslän, as *G. locusta*, 2 imm., with 2 adult *G. locusta* (B.M. 97.6.1.33, part).

**Norway**

W. NORWAY. Bergen (near), Molde, 19. vi. 39, G.I.C., 1♂, 11 yng ♂♂ and imm. (B.M. 1942.8.5.73–77). N. NORWAY. Tromsö, 30. vi. 39, half-tide, G.I.C, 15 advanced imm. (B.M.). Lofoten Is., Svolvaer, 26. vi. 39, mid-tide, G.I.C., 1 imm. Skaervoy, S. of Hammerfest, 2. vii. 39, half-tide, G.I.C., 10♂♂, 6♀♀, 10 imm. (B.M., 1942.8.5.51–55). Malangen, Nordbotten, vii. 1881, Cop.Mus., ♂ and ♀ (with *G. setosus*). Porsangerfjord, Honningsvåg, 5. vii. 39, mid-tide, G.I.C., 2♂♂, 2 imm. (with *G. duebeni* and *Marinogammarus finmarchicus*) (B.M.). Porsangerfjord, Rimabukt, 10. vii. 39, L.W. to half-tide, G.I.C., large ♂. Porsangerfjord, Suogalma, 6. vii. 39, L.W. to half-tide, G.I.C., 6♂♂, 8♀♀ (7 ovig.), *c.* 65 imm. and yng adults (B.M. 1942. 8.5.44–50). Lang Fjord, Finmark, as *G. locusta*, Norman Coll., 1 imm. (B.M. 1911.11.8.18852).

**Iceland**

E. ICELAND. Berufjörður, 0–3 m., 14. vii. 1900, Cop.Mus., 2♂♂ and 1♀ (with other spp.), shore, below 'ordinary high water'. Loðmundarfjörður, 9. v. 1898, Cop.Mus., 7♂♂, 6♀♀, 2 imm. 'midtfjords i bunden, 13 m. St. 7'. S.E. ICELAND. Hornafjörður shore, 29. viii. 36, Cop.Mus., 6♂♂, 1♀, 19 imm. W. ICELAND. Hvammsfjörður shore, 19. vii. 1886, Cop.Mus., 6♂♂, 6♀♀, many imm.

**Spitzbergen**

As *G. locusta* var. *zaddachi*, A. Schellenberg det., 2 large ♂♂ of 34 and 35 mm., 6 imm., with *G. setosus* (B.M. 1934.9.1.21–24, part).

**Greenland**

E. GREENLAND. Angmagssalik, 4 m., 10. viii. 33, Cop.Mus., 1♂, 1♀ (with *G. setosus* and *G. wilkitzkii*). Angmagssalik, Tasiusak, Cop.Mus., large ♀ [nec *setosus*]. 'GREENLAND'. 7♂♂, 1♀, ex coll. Cop.Mus. S.E. GREENLAND. Lindenowsfjord, 50–75 m., 28. vii. 35, Cop.Mus., 2♂♂, 3♀♀ (not breeding) (with *G. setosus*). W. GREENLAND. Holsteinsborg, ex coll. Cop.Mus., 5♂♂, 6♀♀, 9 imm., (breeding actively) (with *G. setosus*). Holsteinsborg, N. Strömfjord, 1911, Cop.Mus., 6♂♂, 3♀♀ (with *G. setosus*). Waigat, Sakkrak, 1892, 5♂♂, 2♀♀, Cop.Mus. Upernavik, 12. vi. 36, Cop.Mus., ♂. Davis Strait, 63° 27′ N, 54° 12′ W., E. Whymper, (B.M. 79.26 as '*locusta*'), 1♀, not breeding, with several juvenile *G. wilkitzkii*.

**N. America**

CANADA, QUEBEC. Lac Tadoussac, July 1938 (V.D.V.), per G.I.C., 6 large ♂♂, largest 31 mm. NEWFOUNDLAND, 1885, per E. W. Sexton, adult ♂♂. NOVA

SCOTIA. Off Halifax, loc. 74, 1881, U.S. Fish. Comm., '*G. ornatus* Edw.', Norman Coll. as '*locusta*' (B.M. 1911.11.8.18929–932), 3 ♂♂, 1 ♀. MASSACHUSETTS. Gloucester Harbour, U.S. Fish. Comm., '*G. ornatus* Edw.', Smithsonian Inst., (B.M. 80.26 as *locusta*), 1 ♂ (*c.* 34 mm.), 1 ♀ with brood. CONNECTICUT. New Haven, '*G. ornatus* Edw.', S. I. Smith, Norman Coll. as '*locusta*' (B.M. 1911.11.8.18919–928), 4 ♂♂, 11 ♀♀, (most ovig.). 'N.E. AMERICA'. '*G. ornatus* Edw.', S. I. Smith, Norman Coll. as *locusta* (B.M. 1911.8.18933–937), 2 ♂♂, 4 ♀♀ (not breeding).

## APPENDIX II

### *Re-identifications from the Literature*

### DEMENTIEVA (1931)

At the time this paper was written all northern marine *Gammarus* were still referred to *G. locusta*, but it was realized that much variation existed. Dementieva's biometric data aimed at expressing the differences between certain selected populations in a more precise form. Her results enable these populations to be identified. She rightly concluded, incidentally, that her 'typical forms' (*zaddachi oceanicus*) and 'brackish-water forms' (*setosus*) were distinct species.

| Population | Dementieva's name | Data or illustrations | Re-identification |
|---|---|---|---|
| Kola Gulf (Murmansk) | *G. locusta* 'typical forms' | Tables 5, 7; figs. 7*a*, 8*a*, 12*a–c* | *G. zaddachi oceanicus* Seg. |
| Baltic Sea | *G. locusta* 'typical form' | Table 7; table on p. 77 (left col.) | *G. zaddachi oceanicus* Seg. |
| Belouchia Bay (Novaya Zemlya) | *G. locusta* 'brackish-water form' | Tables 5, 6; figs. 7*b*, 8*b*, 12*a–c* | *G. setosus* Dement. |
| Zabloula Bay (Novaya Zemlya) | *G. locusta* 'brackish-water form' | Figs. 7*c*, 8*c*; table 6 | *G. setosus* Dement. |
| Barents Sea | *G. locusta* 'deviating form' | Table on p. 76; fig. 9 | *G. wilkitzkii* Birula |
| Baltic Sea | *G. locusta* 'deviating form' | Fig. 10; table on p. 77 (right col.) | *G. zaddachi zaddachi* Spooner |
| Kola Bay, etc. | *G. duebenii* | Figs. 11, 12*a*, *b* and *e* | *G. duebeni* Lillj. |

*G. zaddachi oceanicus* is the 'typical' form characteristic of the Kola Gulf shore, where it is not normally mixed with *G. setosus*. When it extends into shallow arms of the sea diluted with river water or land drainage it may overlap the range of *G. duebeni*. In Novaya Zemlya, *G. z. oceanicus* is reported from the seaward end of the bays visited, in which it tends to be replaced by *G. setosus* in shallower and fresher parts. In Mituschikha Bay both occurred together at the same depth. In the north Baltic, *G. zaddachi oceanicus* and

*G. zaddachi zaddachi* occur together, as is now well known from Segerstråle's investigations. *G. z. oceanicus* of the Baltic are smaller than those of such typical habitats as the shore of Kola Bay, and their limbs are a little stouter.

### Gurjanova, E., Sachs, S. & Uschakow, P. (1929)

The *G.* '*locusta*' from Kola Bay, referred to in this paper may be taken to refer to *G. z. oceanicus*. *G. setosus*, as we now know, is quite scarce in this area, and *G. locusta* (s.s.) scarcely reaches it and is at best very rare.

### Gurjanova, E. (1929)

*G.* '*locusta*' is reported as 'everywhere in large numbers, littoral'. In this area, Cheshskaya Bay, conditions are rigorous and only euryhaline and eurythermal species survive. This must be chiefly *G. zaddachi oceanicus*, if not entirely. At most a minority may be *G. setosus*.

### Gurjanova, E. (1931)

Amongst the amphipod fauna of the east Murmansk coast (Portschnicha Bay) *G.* '*locusta*' is described as a characteristic littoral species. (*G. wilkitzkii* is now clearly distinguished.) Since *G. setosus* proves to be quite scarce on this coast, the remarks can be taken as referring to *G. zaddachi oceanicus*.

### Gurjanova, E. (1932)

By the time of publication of this paper (and perhaps earlier) Gurjanova already distinguished *G. setosus* as separate from *G.* '*locusta*', and refers to it as *G. locusta* var. *mutata*.

In an account of the fauna of that obscure and peculiar region off the Siberian coast known as Nordenskjöld's Sea (or the Sea of the Brothers Laptev), records are given of two of the three arctic *Gammarus*.

| Gurjanova's name | Re-identification | Occurrence |
|---|---|---|
| *G. locusta* | *G. zaddachi oceanicus* | 73° 05′ N., 140° 45′ E., 16·5m., 0·42° C., 2 ex<br>73° 20′ N., 139° 08′ E., 16 m., 0·45° C., 1 ex<br>'also previously from ten other stations in the region of the New Siberian Islands' |
| *G. wilkitzkii* | *G. wilkitzkii* | 72° 9′ N., 135° 45′ E., 20 m., 0·3° C. |

Note that Popov (1932), in describing the conditions of life in the Brothers Laptev Sea, refers to '*G. locusta*' being spread all along the littoral of the Siberian coast, and indeed as being the only littoral marine animal! There is virtually no tide here (a few inches at best); the temperature is always minus, and the water has greatly reduced salinity owing to the inflow of several large rivers, including the Lena. Presumably this must be taken to cover *G. zaddachi oceanicus* and *G. setosus*, since the latter was eventually reported from the Laptev Sea, and would be chiefly coastal.

### GURJANOVA, E. (1936)

Further records are given of *Gammarus* from the Nordenskjöld Sea and from the Kara Sea. *G. setosus* is now distinguished specifically. References to *G.* '*locusta*' now refer solely to *G. zaddachi oceanicus*. It is recorded from a station 69° 25′ N., 67° 15′ E. (shore of the Kara Sea).

*G. setosus* is reported from the Laptev Sea for the first time (74° 50′ N., 112° 50′ E.).

### STEPHENSEN (1940*a*)

This is the first occasion on which it is recognized that differences exist between the *G. locusta* of temperate and south Europe, and the form which still passed under the name of *locusta* from the north. The full extent of difference is, however, not appreciated, and the name *locusta* is still retained for both. In so far as the records here quoted are Stephensen's own determination it is possible to distinguish between true *G. locusta* and *G. zaddachi oceanicus* (= Stephensen's northern form of *locusta*).

It is made clear that *G. locusta* (s.s.) ranges into Denmark, but is usually not found farther to the north. In Norway it occurs, but is scarce, and records are given for Oslo fjord; Evenskjaer; Vannøy; and Loppa (*c.* 70½° N.) (p. 318). In fig. 40, II and III apply to *G. locusta*.

The remaining records (unless simply quotations from literature) refer to *G. zaddachi oceanicus*, as does fig. 40 I. The records may be summarized as follows: south and west Norway, several samples from Oslo fjord to Trondheim fjord; north Norway, numerous samples all along the coasts of mainland and islands, to the frontier; Bear Island, in one sample; west Spitsbergen, in Grieg's material; north-east Spitsbergen, at 80° 40′ N.

It is clear that all along the Norway coast *G. zaddachi oceanicus* is far more numerous than *G. locusta*.

*G. setosus* is treated separately, under the name of *G. locusta setosus*. There are three records from the Norway coast, on which it is clearly very scarce; and others from west Spitsbergen; north-east Spitsbergen; Greenland and Arctic America.

*G. wilkitzkii* is recognized as a distinct species, but Stephensen holds that it is possibly synonymous with *G. zaddachi* [= *G. z. zaddachi*] of which it would be a large-sized Arctic representative. A discussion on this topic (pp. 334–6) points out the difficulties in finding qualitative differences 'which cannot be explained as being due to the ordinarily very great difference in size'. Stephensen, however, minimizes the real differences in the antennal setation, the significance of the relative elongation of several limb segments, and of the long uropod 3 inner ramus. Moreover, he entirely ignores the diagnostic propod of female gnathopod 2, which is quite unlike that of *G. zaddachi.* There is no question that *G. wilkitzkii* is separate from *G. zaddachi.*

### STEPHENSEN (1940*b*, 1944)

In these excellent accounts of the amphipod faunas of Iceland and east Greenland, all *G. locusta* s.s. refer to *G. zaddachi oceanicus*, and *G. locusta setosus* to *G. setosus.*

In Iceland, *G. z. oceanicus* is the form which attains an 'enormous frequency' and is recorded all round the coast. Recently the true *G. locusta* has been found to occur (Segerstråle, 1950); but evidently it was not seen by Stephensen, and must be very scarce, being at the extreme northern limit of its range. *G. setosus* occurs fairly freely round the Iceland coast, more freely than in Norway, but is clearly outnumbered by *G. z. oceanicus* (see 1940*b*, pp. 56–8 and fig. 7).

In Greenland the occurrence of *G. z. oceanicus* is proved on the east coast northward to Hvalrosodden (77° N.). Other information exists to show it occurs on the west coast to at least 73° N. (material identified by Dr Segerstråle or myself). Judging, however, from the numbers and sizes of specimens recorded, it may be concluded that *G. z. oceanicus* flourishes less in Greenland than in Iceland or Norway, and is considerably outnumbered by *G. setosus.* It is *G. setosus* now which attracts attention from its numbers, e.g. at Angmagssalik it 'occurs everywhere on the coast, both on rock facies and on sediment shares found at river mouths'. A difference in the bathymetric range of the two forms is noted, confirming Dementieva's (1931) records from Novaya Zemlya, namely that *G. setosus* in east Greenland is 'a character form of the tidal zone, only exceptionally at depths of more than a few metres', while *G. z. oceanicus* was taken mostly in shallow water from low-water mark downwards to about 20 m., rarely still deeper (50–75 m.) (see 1944, pp. 108–12; fig. 8).

# THE DETERMINATION OF SILICATE IN SEA WATER

By F. A. J. Armstrong
Experimental Officer at the Plymouth Laboratory

(Text-figs. 1–3)

Silicon in sea water may be present in suspension, in particles of clay or sand, as a constituent of diatoms, etc., or in solution. Some silicon in solution occurs in the form of silicate. This is usually estimated by the colorimetric method of Diénert & Wandenbulcke (1923), which makes use of the yellow colour of the silicomolybdic acid which is formed when ammonium molybdate and sulphuric acid are added to the water (Atkins, 1923). The colour may be compared with that of standard solutions of picric acid (Diénert & Wandenbulcke, 1923) or potassium chromate (Swank & Mellon, 1934). The method is simple but the colour in sea water is often faint and is not easy to match visually, nor is its intensity strictly proportional to the concentration of silicate. Less colour is produced in sea water than in standard solutions made with distilled water and this 'salt error' must be allowed for (Brujewicz & Blinov, 1933; Wattenberg, 1937; Robinson & Spoor, 1936).

The work described below was done in an attempt to apply to sea water the more sensitive method in which silicomolybdic acid is formed and then reduced to molybdenum blue, a method which is now often used for determining trace amounts of silicon in other materials. It was found that this could be done, and an analytical method devised which would allow the determination of silicate in a range of concentrations from 0·1 to 50 $\mu$g. atoms Si/l.

The method adopted is based upon the results of an investigation of the properties of silicomolybdic acid by Strickland (1950), which are summarized below.

Strickland found that when silicic acid reacts with molybdate, two forms of silicomolybdic acid may be formed, depending on the degree of acidification of the molybdate. When the normal molybdate ion is acidified with 1·45 to 1·50 equivalents of acid per g. ion of $MoO_4^{--}$, then the silicomolybdic acid described in the literature is the main product of the reaction. He terms this $\alpha$-silicomolybdic acid to distinguish it from the other form, which he calls $\beta$-silicomolybdic acid, produced when silicic acid reacts with molybdate acidified with more than about 2 equivalents of acid per g. ion of $MoO_4^{--}$. He states, further, that the presence of much electrolyte in solution decreases the ratio of $\beta$- to $\alpha$-compounds formed at a given acidity. Moreover, over a period of several hours the $\beta$-form changes spontaneously and irreversibly into the $\alpha$-form. The $\beta$-compound has apparently the same empirical formula as the $\alpha$-compound and has a similar but more intense yellow colour, the extinction for a given quantity of combined silica being over twice as great.

These findings, which I have confirmed, are consistent with reports in the literature of non-reproducibility and fading of the colour.

Strickland also investigated the reduction of these compounds by stannous chloride. In the presence of excess molybdate, both form blue compounds, but of different appearance and absorption spectra. That from the α-acid, which is greenish blue, has over 1½ times the molecular extinction coefficient of that from the β-acid, which is royal blue.

For analytical use Strickland recommends preparation of the β-compound as more reproducible, and for this purpose it is necessary to acidify the molybdate with between 3 and 5 equivalents of acid. A concentration of molybdate, such that [Mo] = 0·5 M remains after the silica has combined, is suitable for all concentrations of silicate, but the ionic strength of other ions must not exceed 0·5 M. Formation of the complex is complete in 5–10 min., and absorption measurement or subsequent reduction should not be delayed for longer than a further 15 min.

It is also known that for reduction, the stannous chloride may not be added immediately to these weakly acid solutions, or the excess molybdate will be reduced to a blue compound. If, however, the solution is first made approximately 1 N with HCl, or 1·5 N with $H_2SO_4$, the excess molybdate is converted rapidly (in about half a minute) into a form which will not reduce to a blue. Upon addition of stannous chloride only the silicomolybdic acid is reduced to molybdenum blue, but some of the excess molybdate is reduced to a substance of brownish yellow colour, probably a quinquevalent molybdenum compound. The amount of this increases with increasing molybdate, chloride, and stannous chloride concentrations. This compound has a measurable light absorption with the red light-filters used for measurement of absorption of molybdenum blue, and contributes to the 'reagent blank' of the method.

## EXPERIMENTAL

Extinctions of coloured solutions were measured with the absorptiometer already described (Harvey, 1948). With it extinctions up to 0·5 can be measured to the nearest 0·001, and it will accommodate cuvettes of up to 25 cm. length. The distilled water used was prepared in a still having a silver condenser and was assumed to be silicon free.

As a basis for comparison the Diénert-Wandenbulcke method, as adapted by Atkins, was used, and series of solutions with known additions of silicon as silicate were prepared from distilled and sea water. To 100 ml. portions of these were added 2 ml. of 10% ammonium molybdate and 4 drops of 50% v/v sulphuric acid. The extinctions of the resulting yellow solutions were measured in a 20 cm. cuvette with Chance OB 1 (blue) and then with Ilford 601 (violet) filters in the absorptiometer. The results are shown in Fig. 1 A. It will be seen that the relationship between extinction and silicon concentration is not linear, though the curvature is less with the 601 filter (which transmits light of shorter wave-length) and the sensitivity is greater. The decrease in sensitivity in sea water is also to be seen.

A test of the molybdenum-blue method was made as follows. In each of a series of 100 ml. flasks 5 ml. of 5% ammonium molybdate and 3 ml. 1 N-hydrochloric acid was placed, and 25 ml. of distilled or sea water containing

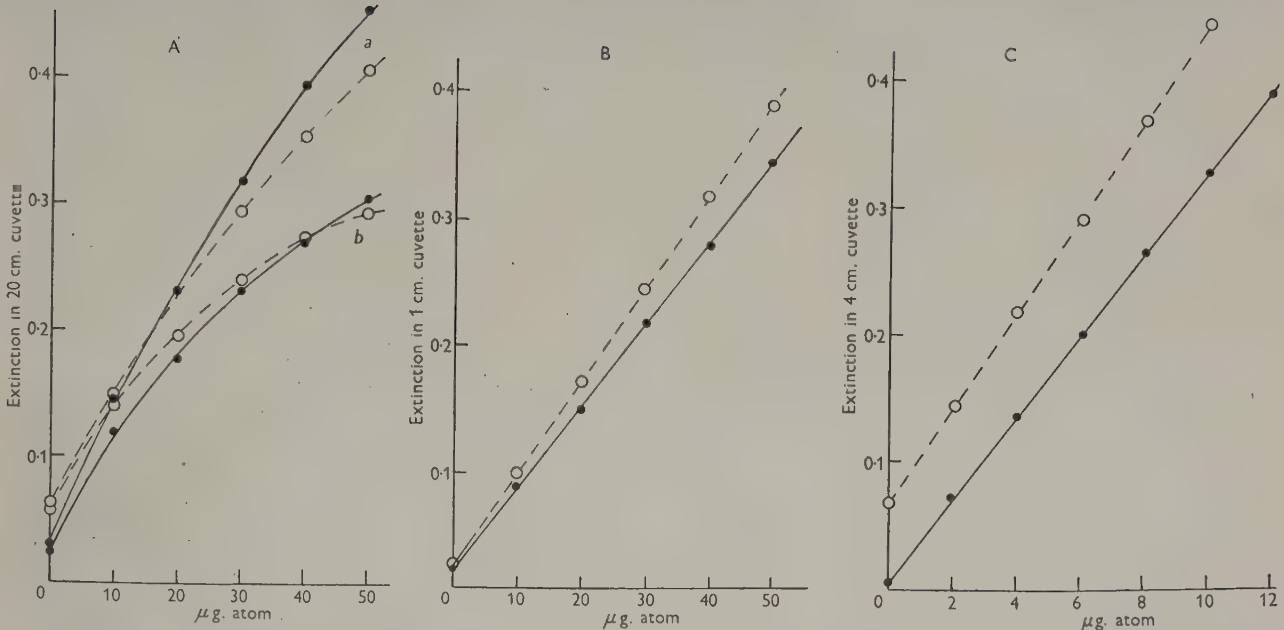

Fig. 1. The relation between extinction and silicate concentration (A) with the Diénert-Wandenbulcke method; (B) with the molybdenum-blue method; (C) with the molybdenum-blue method, quantity of molybdate reduced. Silicon added (horizontal scale) in μg. atom Si/l. *a*, Ilford 601 filter (violet); *b*, Chance OB 1 filter (blue). Continuous line, distilled water; broken line, sea water.

known additions of silicon were added. After 10 min. 5 ml. of 35% v/v sulphuric acid were added, the solution allowed to stand 5 min., and 1 ml. 0·1 N-stannous chloride added. After a further 10 min. the extinctions of the solutions were measured in a 1 cm. cuvette, using Chance OR 1 (red) filters. These were used because they are already in use for phosphate determinations; Ilford 608 Spectrum Red filters are equally suitable. The results are shown in Fig. 1 B, which displays the linearity of the relationship between extinction and silicon concentration. The sensitivity in sea water is greater, indicating that some α-silicomolybdate has been formed.

The molybdenum-blue method is thus about 16 times more sensitive than the older procedure. The advantage cannot, however, be exploited by using a longer cuvette to increase extinction values unless the reagent blank (which would increase proportionally) can be decreased. With distilled water with no added silicon the extinction is 0·015, which is equivalent to about 2 μg. atoms Si/l.

As a first step toward reducing the blank, a method of eliminating interference from phosphate and arsenate was tried. (There are usually a few parts per million of phosphate in the reagents which contribute to the blank.) In sea water the concentrations of phosphate and arsenate are normally negligible in comparison with that of silicate. An experiment showed that with the procedure given above, equal extinctions were produced by 101 μg. of Si as silicate, 85 μg. P as phosphate, and 235 μg. As as arsenate. It has been shown (Denis & von Meysenbug, 1922; Bordeionu, 1927; Riehm, 1932) that oxalic (or citric or tartaric) acids will suppress interference from phosphate and arsenate. A trial showed that the addition of 2 ml. of 10% oxalic acid to the solution after acidification with sulphuric acid completely suppressed the formation of molybdenum blue from added phosphate and arsenate, leaving the extinction caused by silicate unchanged. The blank extinction decreased to 0·012.

A further decrease should result if the amounts of molybdate and stannous chloride could be reduced, and was realized by the following procedure.

In a 100 ml. flask were placed 50 ml. of the sample, and 2 ml. of a reagent made by mixing 5 vol. of 5% ammonium molybdate and 3 vol. of 1 N-hydrochloric acid. After standing 10 min., 5 ml. of 50% sulphuric acid and 2 ml. of 10% oxalic acid were added and the extinction measured in the absorptiometer, using a 4 cm. cuvette. (This gave a measure of the natural turbidity of the solution, to be subtracted from the final reading to give a true measure of the colour produced.) Ten min. after acidification 1 ml. of 0·05 N-stannous chloride was added, and the extinction measured after a further 15 min.

Results for known additions of silicon to distilled water and to a sample of sea water comparatively low in silicate are shown in Fig. 1 C. The plots remain linear; the slope, indicating sensitivity, being greater for the sea water. The blank for distilled water, of 0·007, represents a concentration of 0·19 μg.

atom Si/l. The reagent blank in sea water, which is greater than in distilled water because the high concentration of chloride causes increased formation of the yellowish quinquevalent compound, cannot be found directly unless silicate-free sea water can be obtained. The silicon content of the sample of sea water is not given by this experiment. The way in which the blank is found is described below.

As was mentioned above, the blank has two components, molybdenum blue due to silicon in the reagents, and the quinquevalent molybdenum colour due to reduction of excess molybdate. Provided that it is small the correction for silicon in the reagents is the same in distilled water and in sea water. The quinquevalent molybdenum colour is, however, greater in water containing chloride. It may be found directly by making the solution strongly acid before adding the molybdate; in 1·5 N-acid solution silicate will not combine with molybdate, and on adding stannous chloride the only colour produced is that due to reduction of excess molybdate.

Three measurements will then allow the blank correction for sea water to be calculated: (i) the extinction with silicon-free distilled water carried through the normal procedure; (ii) the extinction with distilled water when the 5 ml. 50% v/v sulphuric acid is added before the molybdate reagent, addition of oxalic acid and stannous chloride following as usual; (iii) the extinction with sea water carried through the procedure of (ii) above.

The difference between measurements (i) and (ii) is the extinction due to silicate in the reagents, and must be added to measurement (iii) to obtain the total blank correction. This is to be subtracted from extinction measurements made upon sea water.

The method at this stage of development was put into use for silicate determinations on samples of sea water, and was found to work fairly well, although the reproducibility of calibration with known additions of silicate was not entirely satisfactory. More disturbing was the occurrence of occasional high figures as if contamination had taken place. This effect was traced to attack of the resistance glass of the flasks by the sea water before addition of the molybdate reagent, and was surprisingly large. Several micrograms of silicon were dissolved in 30 min. It was found that placing the molybdate reagent in the flask first and then adding the sea water prevented this, presumably because the solution was now acid instead of faintly alkaline.

Variations in calibration figures were thought to be due to variation in the proportion of α-silicomolybdate formed, and so should be reduced if this could be decreased. The difference in the slopes of the lines in Fig. 1 B indicates that about 30% of the silicomolybdate formed in sea water is in the α-form. An increase of the acidity of the reagent to the maximum recommended by Strickland was therefore tried, the reagent being made by mixing 2 vol. of 5% ammonium molybdate and 3 vol. of 1 N-hydrochloric acid. When 3 ml. of this reagent was used (in place of the 2 ml. previously employed) the sensitivity in sea water was nearer to that in distilled water, and corresponded to about 12% α-silicomolybdate formation. In subsequent routine use the calibration factors with this reagent were satisfactorily constant.

The data obtained so far were got in a laboratory at fairly constant temperature, and care had been taken to adhere to the stated timing. The usefulness of the method would be increased if it were known what latitude could be allowed, and a few experiments were done to find this out.

Fig. 2A shows the effect of temperature upon the depth of colour produced by a given quantity of silicate, the temperature being that at which the sea water and molybdate were allowed to react, the solutions being brought to 20° C. for the rest of the procedure. It is seen that the change in extinction with temperature is about 2 parts/1000/° C.

Fig. 2B shows the effect of altering the time of interaction (at 18° C.) of the sea water and molybdate, i.e. the time between addition of the sample and acidification with sulphuric acid. The maximum extinction is produced after 10–15 min.

Fig. 3 shows the development and subsequent fading of colour at temperatures of 13 and 22° C. The upper curves are of extinctions with (different) samples of sea water and represent the colour due to the combined effect of the molybdenum blue and the quinquevalent molybdenum blank, while the lower line is that of the latter alone, which was the same at both temperatures. The colour reached a maximum after 60 min. at 13° C. and after 30 min. at 22° C. and was within 1% of this maximum between about 40 and 70, and 16 and 32 min. respectively. In distilled water the colour attains its maximum within 3–5 min. and is constant for about 3 hr. at 20° C.

These times are longer than had been allowed in the earlier experiments, and have been used as a guide in subsequent work.

## Recommended Procedure

*Solutions required*

(1) Ammonium molybdate, 5% w/v.
(2) Hydrochloric acid, 1 N.
(3) Sulphuric acid, 50% v/v.
(4) Oxalic acid, 10% w/v.
(5) Stannous chloride, 0·05 N.
(6) Standard silicate solution.

The ammonium molybdate and hydrochloric acid solutions should be prepared from A.R. grade materials and silicon-free distilled water, and kept in polyethylene, ceresin, or heavily waxed bottles. The mixed reagent for use, consisting of 2 vol. molybdate and 3 vol. acid, should be freshly prepared, as it sometimes throws down a precipitate on standing for 1 or 2 days.

The stannous chloride is conveniently made just before it is required, by dilution from a stock solution of, say, 40 g. $SnCl_2.2H_2O$ in 100 ml. 50% v/v HCl.

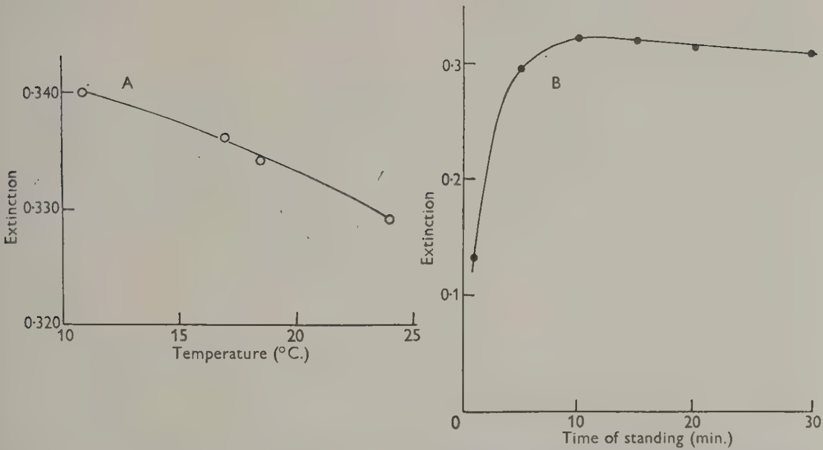

Fig. 2. A, The effect of temperature upon the amount of molybdenum blue formed, in sea-water. Extinction in 4 cm. cuvette given by about 10 $\mu$g. atoms Si/l. B, The effect of time upon the interaction of silicate and acid molybdate. Extinction in 4 cm. cuvette.

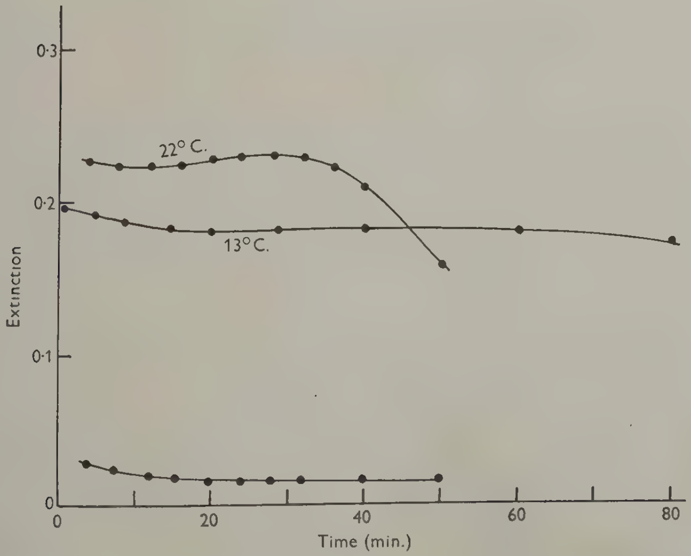

Fig. 3. Changes in the extinction of sea-water solutions with time. The lower line shows the quinquevalent molybdenum blank, which was the same at the two temperatures used.

The exact strength may be between 0·04 and 0·06 N, and is not important provided that the same solution is used for both the blanks and the determinations.

A standard silicate solution may be prepared by fusing 0·1201 g. silica with 0·6 g. anhydrous sodium carbonate, and dissolving the melt when cold in water, and making to a volume of 100 ml. This solution contains 20 $\mu$g. atoms Si/ml., and can be diluted serially for use. If kept in a well-stoppered polyethylene bottle, it is stable for at least a year. As a source of silica, finely powdered 'Vitreosil' is suitable. It should be heated to redness and cooled in a desiccator before weighing, and contains over 99·8% $SiO_2$.

### *Apparatus required*

The absorptiometer used in these experiments is very convenient, but is only essential if the lowest silicate concentrations have to be measured. For concentrations greater than about 0·5 $\mu$g. atom Si/l. the 'Spekker' instrument of Messrs Adam Hilger, or one of the other photoelectric absorptiometers capable of holding a 4 cm. cuvette, would serve. The method can of course be used with a visual absorptiometer or with Nessler cylinders with a small loss of precision and speed. With the latter a comparator system would be necessary because of the mixture of blue and yellow colours.

Polyethylene bottles are desirable for samples and some reagents. Ordinary (grade B) pipettes may be used for measuring out the reagents. A 50 ml. graduated cylinder is suitable for the sea-water sample.

### *Determination*

Three ml. of the mixed acid molybdate reagent are placed in a 100 ml. flask and 50 ml. of the sample added. After 10 min. 5 ml. of 50% sulphuric acid and 2 ml. of 10% oxalic acid are added. The extinction of the solution in the absorptiometer is measured using deep red filters. The length of the cuvette should suit the silicon content (see below). Five minutes after acidification 1 ml. of 0·05 N-stannous chloride is added, and the extinction is measured again after a further 20–40 min. depending upon the temperature.

The difference between these two readings must be corrected for the blank which is determined as described on p. 153.

Calibration is carried out by measuring the increase in extinction produced by a known addition of silicate to a sample of sea water of low silicon content. If such a sample is not available, 3·5% w/v sodium chloride may be used without an error of more than 1 or 2%.

Since the extinction/concentration relationship is linear a factor may be used to convert corrected extinctions to silicon content. For example, with a 4 cm. cuvette, an extinction of 1·00 corresponds to about 27 $\mu$g. atoms Si/l. Using an absorptiometer which measures extinctions up to 0·5, the cuvette lengths suitable for different ranges of silicon concentrations are as follows:

| Concentrations (μg. atoms Si/l.) | Cuvette length (cm.) |
|---|---|
| 0·1–0·5 | 10 |
| 0·25–12·5 | 4 |
| 1·0–50 | 1 |

A worked example will illustrate the method of calculation. With a 4 cm. cuvette, the following extinctions were obtained.

### Blank

Distilled water, normal order of addition of reagents;

| | |
|---|---|
| Before adding stannous chloride | 0·000 |
| After adding stannous chloride | 0·006 |

Distilled water, $H_2SO_4$ added before molybdate:

| | |
|---|---|
| Before adding stannous chloride | 0·000 |
| After adding stannous chloride | 0·004 |

The extinction due to silicon in the reagents is therefore 0·006 − 0·004 = 0·002.

Sea water, $H_2SO_4$ added before molybdate:

| | |
|---|---|
| Before adding stannous chloride | 0·007 |
| After adding stannous chloride | 0·013 |

The quinquevalent molybdenum blank for sea water is therefore 0·013 − 0·007 = 0·006, and if to this is added 0·002 for the silicon in the reagents, the total 0·008, is the blank to be subtracted from measurements on sea water.

### Calibration

Sea water, normal addition of reagents:

| | |
|---|---|
| Before adding stannous chloride | 0·005 |
| After adding stannous chloride | 0·048 |

The same sea water, to which 10·0 μg. atoms Si/l. have been added:

| | |
|---|---|
| Before adding stannous chloride | 0·005 |
| After adding stannous chloride | 0·420 |

The extinction due to the addition of 10·0 μg. atoms Si/l. is thus (0·420 − 0·005) − (0·048 − 0·005) = 0·372, so that an extinction of 1·00 corresponds to $10{\cdot}0 \times \frac{1{\cdot}00}{0{\cdot}372}$ or 26·9 μg. atoms Si/l.

### Sample

Sea-water sample, normal order of addition of reagents:

| | |
|---|---|
| Before adding stannous chloride | 0·006 |
| After adding stannous chloride | 0·281 |

The extinction for the sea water, corrected for turbidity, is thus 0·281 − 0·006 or 0·275, and from this figure 0·008 must be subtracted for the total blank, leaving 0·267.

The silicon content of the sample is then 0·267 × 26·9 or 7·18 μg. atoms Si/l.

### Reproducibility

Replicate analyses usually agree within ± 3 %. Five analyses of a sample of sea water gave the following results: 11·53, 11·55, 11·61, 11·61, 11·63 μg. atoms Si/l.

### Time needed

Analysis of ten samples, with blanks and calibration, may be done in about 2 hr. Calibration is needed only occasionally.

### Storage of samples

Samples should be collected in polyethylene or heavily waxed bottles, and kept in the dark to prevent multiplication of diatoms, which may consume silicate. They should not be kept long before analysis, since suspended siliceous matter may dissolve forming soluble silicate. A series of samples gave the following figures before and after storage for 3 months:

| Date of analysis | Silicate (µg. atoms Si/l.) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 28. viii. 50 | 19·0 | 2·45 | 0·94 | 1·12 | 0·79 | 0·56 | 0·47 | 0·47 | 1·91 | 2·12 | 2·34 |
| 17. xi. 50 | 15·6 | 2·47 | 1·06 | 1·27 | 1·01 | 0·80 | 0·83 | 0·81 | 2·19 | 2·30 | 2·66 |
| Increase (%) | −18 | 1 | 13 | 13 | 28 | 43 | 77 | 72 | 15 | 9 | 14 |

Dr W. R. G. Atkins (private communication) has found a similar increase in the silicate content of samples of sea water stored in polyethylene bottles for about the same time.

## Some Results

Samples from the surface at the Laboratory Stations L 2 to L 6 and from various depths at International Hydrographic Station E 1 have been analysed by this method since March 1950, with the results given in Table I. They show high values at the surface near Plymouth, due to land drainage, decreasing with distance off-shore, although the effect is noticeable 12 miles out. They show, too, the depletion of silicate in the upper layers at E 1 in the summer months, as observed here in earlier years. (Atkins, 1923–30; Cooper, 1933). On 3 May silicate was low throughout the water column. The samples had been taken after a spell of rough bright weather, during which it is probable that vertical mixing carried silicate depletion to all depths. Phosphate was also low at all depths. The change in silicate concentration only 3 weeks later is notable.

Table I. Silicate Off-shore from Plymouth (µg. atoms Si/l.)

| Station | Miles from laboratory | Depth (m.) | 24 Mar. | 3 May | 23 May | 12 June | 19 July | 23 Aug. | 20 Sept. | 23 Oct. | 22 Nov. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| L 2 | 2 | 0 | — | 1·03 | — | — | 1·98 | 19·0 | 6·13 | 7·61 | 22.0 |
| L 3 | 5 | 0 | — | 1·06 | — | — | 0·87 | 2·45 | 5·03 | 3·60 | 10·2 |
| L 4 | 8 | 0 | — | 0·87 | — | — | 0·87 | 0·95 | 3·04 | 2·00 | 4·49 |
| L 5 | 12 | 0 | — | 0·94 | — | — | 0·89 | 1·12 | 1·06 | 1·81 | 4·83 |
| L 6 | 17 | 0 | — | 0·62 | — | — | 0·95 | 0·79 | 1·04 | 1·73 | 3·04 |
| E 1 | 22 | 0 | 2·63 | 0·48 | 1·17 | — | 0·69 | 0·56 | 0·69 | 1·82 | 2·76 |
| E 1 | 22 | 5 | 2·63 | 0·39 | 1·38 | — | 0·78 | 0·47 | 0·67 | 1·75 | 2·71 |
| E 1 | 22 | 10 | 2·38 | 0·54 | 1·37 | 1·51 | 0·89 | 0·47 | 0·61 | 1·79 | 2·69 |
| E 1 | 22 | 25 | 2·63 | 0·73 | 1·74 | — | 2·18 | 1·91 | 0·67 | 1·77 | 2·67 |
| E 1 | 22 | 50 | 2·44 | 0·62 | 2·39 | 1·74 | 2·23 | 2·12 | 1·38 | 1·79 | 2·56 |
| E 1 | 22 | 70 | 2·67 | 0·77 | 2·20 | — | 2·38 | 2·34 | 1·98 | 1·71 | 2·81 |

A series of samples provided by the kindness of Mr R. A. Cox and members of the Staff of R.R.S. *Discovery II* from a position (47° 24′ N. 7° 52′ W.) in the North Atlantic Ocean just off the edge of the continental shelf has been examined, and the results are given here (Table II) because of the scarcity of observations of silicate in deep water in northern latitudes. Atkins & Harvey (1925) report 8 μg. atoms Si/l. at 2000 m. at 37° 44′ N. 13° 21′ W., and 20 at 3000 m. at 29° 59′ N. 15° 03′ W.

TABLE II. SILICATE IN THE NORTH ATLANTIC OCEAN, 47° 24′ N., 07° 52′ W. ON 12 MAY 1950. SOUNDING 4030 M.

| Depth (m.) | Silicate (μg. atoms Si/l.) | Depth (m.) | Silicate (μg. atoms Si/l.) |
|---|---|---|---|
| 0 | 0·78 | 900 | 10·2 |
| 10 | 1·01 | 1000 | 10·8 |
| 20 | 0·52 | 1100 | 11·7 |
| 50 | 1·76 | 1200 | 12·3 |
| 100 | 2·32 | 1500 | 13·3 |
| 150 | 2·6 | 2000 | 19·1 |
| 200 | 2·6 | 2500 | 28·6 |
| 300 | 3·5 | 3000 | 35·6 |
| 400 | 4·8 | 3500 | 38·7 |
| 600 | 7·1 | 3900 | 40·8 |
| 800 | 10·0 | | |

## SUMMARY

A sensitive molybdenum-blue method for determining silicate based on a recent account of the chemistry of silicomolybdic acid has been applied to the analysis of sea water.

Methods of eliminating interference from phosphate and arsenate, and of reducing and evaluating the reagent blank, and some effects of temperature and timing have been studied.

A method is described which may be used with a sensitive absorptiometer for silicate concentrations in the range 0·1–50 μg. atoms Si/l.

Some results obtained with the method are presented, and illustrate change in silicate concentration of sea water on storage, and silicate in the water off Plymouth in 1950, and at a position in the North Atlantic Ocean.

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# AUTECOLOGY AND THE SPECIES PROBLEM IN *FUCUS*

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(Text-figs. 1–6)

On the rocky shores of the British Isles three species of *Fucus* are commonly found as components of the intertidal algal belt, namely, *F. spiralis* L., *F. vesiculosus* L. and *F. serratus* L. A fourth species, *F. ceranoides* L., occurs in places subject to the influence of fresh water but, although it may be important in connexion with the interacting processes to be described below, *F. ceranoides* is omitted from the present discussion because as yet too little is known of its autecology. Under the conditions prevailing in the characteristically zoned algal flora of an undisturbed region of a rocky coast, descriptions of the three species can be applied which fairly effectively distinguish one from the others. The chief characters used for this purpose are shown in Table I.

Other characters also help in separating the three species, as, for example, methods of branching and texture of the frond, and the numbers and positions of cryptostomata; but these characters can be greatly modified by variations in environmental conditions and are difficult to estimate objectively.

## HYBRIDS BETWEEN *FUCUS* SPECIES

Hybrid sporelings between pairs of these species have been produced experimentally a number of times. Thuret (1854) obtained hybrid sporelings by fertilizing eggs of *F. vesiculosus* by antherozoids of *F. serratus*, but failed to make the reciprocal cross. Kniep (1925) carried out the crossing in both directions and obtained 4% development from eggs of *F. vesiculosus* and antherozoids of *F. serratus* and 2% for the reciprocal cross. He obtained much higher percentages of sporelings by crossing *F. spiralis* L. (given as *F. platycarpus* Thur.) with *F. vesiculosus*, 70 and 100% respectively using eggs of *F. spiralis* and *F. vesiculosus* with antherozoids of the opposite species. In February 1949 the present authors obtained 91% segmentation in eggs of *F. serratus* fertilized with antherozoids of *F. vesiculosus* and 99% segmentation for the reciprocal cross. No examples are on record of hybrid plants being grown in culture but this may be due to the difficulty of culturing sporelings of *Fucus* species under laboratory conditions.

The present authors have had some success with trial cultures of *Fucus* sporelings on sterile bricks cemented to the shore. Eggs were released on to the bricks and fertilized by releasing antherozoids over them. The eggs were planted in straight lines for ease of recognition, and the sporelings grown in the laboratory in running sea water for 1 or 2 months, by which time they could easily be seen with the naked eye. The bricks were then cemented to chosen positions on the shore and no difficulty was found in following the growth of the sporelings. On the experimental bricks it was several months before any further sporelings appeared. One difficulty with the method at present is that plantings must be carried out on a large scale to allow for loss of bricks in heavy seas.

TABLE I. CHARACTERS USED IN THE SEPARATION OF *FUCUS SPIRALIS*, *FUCUS VESICULOSUS* AND *FUCUS SERRATUS*

| Character | *F. spiralis* | *F. vesiculosus* | *F. serratus* |
|---|---|---|---|
| Frond: | | | |
| Shape | Spirally twisted | Flat | Flat |
| Vesicles | None | Present | None |
| Margin | Even | Even | Serrated |
| Receptacles: | | | |
| Shape | Rounded | Ellipsoidal-elongate pointed | Extended growth |
| | No dichotomies | 1–2 dichotomies | Several dichotomies |
| Sterile rim | Present | No definite rim | No definite rim |
| Inflation | Inflated | Inflated | Not inflated |
| Sex | Hermaphrodite | Dioecious | Dioecious |

Since hybrid sporelings can be produced quite readily in culture, it might be assumed that they are equally readily formed in the sea, yet very few instances have been recorded of naturally occurring hybrids. Sauvageau (1909), Stomps (1911) and Kniep (1925) recorded plants with characters intermediate between *F. spiralis* and *F. vesiculosus* and assumed that these plants were hybrids. Sauvageau (1909) also described a series of plants intermediate between *F. vesiculosus* and *F. serratus*. The appearance of these plants varied with the position on the shore, approaching *F. vesiculosus* towards the upper limit and *F. serratus* towards the lower limit of distribution. Fritsch (1945, pp. 379–80) remarks, however, 'It still remains doubtful whether these and other transitional types, found at the limits of the zones occupied by the various species of *Fucus*, are actually hybrids or habitat forms'.

Several authors have remarked on this absence of satisfactory hybrid records (Sauvageau, 1909; Kniep, 1925; Fritsch, 1945), and the reason for their relative absence under natural conditions has been attributed to one or other of two causes. (i) Hybrids may really be absent and the suggestion has been put forward that the hybrid sporelings, although formed, find the habitat unsuitable or are unable to compete with the parent species (Kniep, 1925). (ii) Hybrids may really be more common on the shore than is realized, but the extreme variation within the individual species makes it difficult to recognize them with certainty (Sauvageau, 1909).

Thus the three species appear to be fairly distinct from one another, and in addition to the morphological diagnostic features given, others have been used to delimit them as, for example, specific habitat requirements—position on the shore in relation to tide-levels and all that this involves in terms of exposure to desiccation, changing light intensities, temperature and other factors. *F. spiralis* is normally found in the highest position on the shore where it may be left exposed for several days at a time during neap tides; *F. vesiculosus* occupies the mid-tide zone for which it competes with *Ascophyllum nodosum*, and where it is alternately exposed and submerged for each tidal period; *Fucus serratus* occupies the lowest level, and, although part of the zone may be uncovered during the tidal period, other parts may be more or less continually covered.

Recent ecological work has shown, however, that the range of requirements for each of these species is not as limited as was previously supposed. As a result of clearance experiments carried out at different levels on the shore in the south part of the Isle of Man it was shown that removal of one species may allow extension of the ranges of others. In this connexion *Ascophyllum* is important because it dominates the mid-tide region and influences the ranges of all three *Fucus* species. An area cleared in the upper part of the *Ascophyllum* zone, in August 1945 at the time when *Fucus spiralis* was fruiting, became covered by sporelings of the latter species and these persisted and fruited the following year (Burrows, 1947). Further, truncation in December 1943 of *Ascophyllum* plants to a length of 10 cm. over an area of shore allowed development of sporelings of both *Fucus vesiculosus* and *F. serratus* which were present on the rock surface, but which had been prevented from developing by the presence of the *Ascophyllum*. The effect of such truncation on the fucoid component of the area is seen in an analysis of the populations of sample ½ m. quadrats taken towards the end of 1945, one with its lower edge 1 m. vertically below M.S.L. and the other with its lower edge on M.S.L. In each the adjacent ½ m. of uncut *Ascophyllum* area was analysed in order to obtain an estimate of the original composition of the population. Figs. 1 and 2 show percentage frequency distributions for lengths of plants of *Fucus vesiculosus* and *F. serratus* in the sample quadrats. Both species were initially present mainly as sporelings beneath the *Ascophyllum*; at the upper level—zone I—sporelings of *Fucus vesiculosus* were more plentiful and at the lower level—zone II—those of *F. serratus*. In both zones the effect of the removal of the long shading fronds of *Ascophyllum* was to allow continued development of plants of *Fucus serratus* and *F. vesiculosus* and to allow also increase in their numbers.

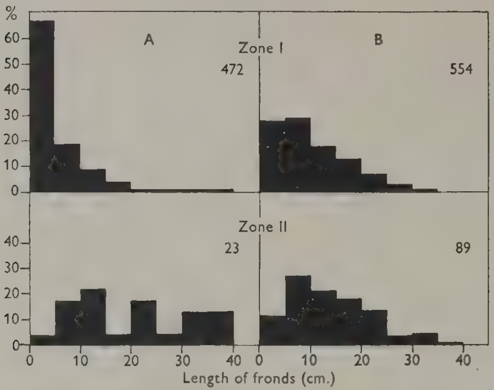

Fig. 1. Growth of *Fucus vesiculosus* 20 months after cutting *Ascophyllum* frondage. A, uncut control; B, *Ascophyllum* cut to 10 cm. Percentage frequency (vertical) of various lengths of *Fucus vesiculosus* fronds (horizontal). The numbers inset give the total number of plants in the sample.

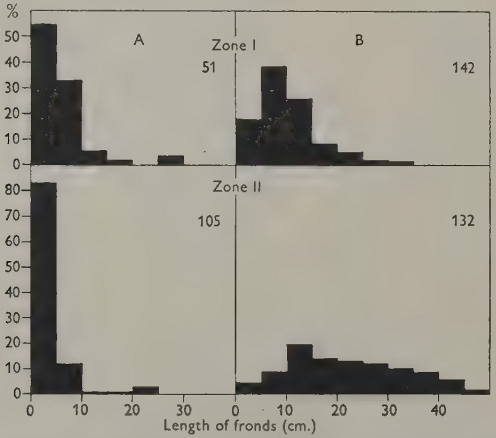

Fig. 2. Growth of *Fucus serratus* 20 months after cutting *Ascophyllum* frondage, as in Fig. 1.

## HYBRIDS ON A RECOLONIZED STRIP

The above facts emphasize the importance of competition in limiting the range of a species. Of extreme interest in this connexion were the results of an experiment carried out on the shore at Port St Mary, Isle of Man (Jones, 1948). A strip, 10 m. wide, extending from just below M.H.W.N.T. to just above M.L.W.S.T., was cleared of limpets and larger algal growth. The experiment was designed to determine the influence on the growth of algae of the large numbers of limpets occurring on the limestone ledges which here bear only an extremely scattered algal population. The area cleared was sufficiently large to eliminate any possible influence of surrounding plants of the parent species. The subsequent development of a dense band of vegetation on the cleared strip has been described by Jones (1948), and the first stages in the succession of algal growth by Lodge (1948). An analysis of the vegetation on the strip after 3 years' growth has been carried out by the present authors. The resultant flora proved to be very different from that expected from previous conceptions of the fucoid zonation of a rocky coast. On the whole, *F. serratus* proved to be more plentiful on the lower part of the strip and *F. vesiculosus* on the upper part, but both occurred at all levels. *F. spiralis* formed no distinct zone but was present in small quantities at all levels down to low-water mark. In this position it was very luxuriant, the fruiting plants having a bushy appearance and a length up to 2 ft. However, the large majority of *Fucus* plants could not be assigned to any one species.

If, as was suggested by Kniep, it is the factor of competition with the parent species which eliminates hybrid sporelings from the shore, then in the absence of competition on a recently cleared area, the occurrence of hybrids might reasonably be expected. An analysis of sample square metres taken from various levels on the strip showed the presence of large numbers of plants which were intermediate in their characters between *F. spiralis* and *F. vesiculosus* (Fig. 3*b*) and between *F. vesiculosus* and *F. serratus* (Fig. 3*a*). For the hybrid analysis Anderson's method (1936), devised for the analysis of hybrid populations of *Tradescantia*, was adopted. The method is briefly as follows—given a number of readily ascertainable characters differing between two species *A* and *B*, for each of these characters an individual plant is given a score, *a*, *b* or *i* depending on whether, in this respect, it follows one or other species or is intermediate between the two. This qualitative scoring can be made quantitative by numerically weighting each of the letters and when the total value for each plant has been computed the indices thus found can be summarized as a frequency distribution. The importance of certain specific characters can be emphasized by appropriate weighting.

### Characters used in the Analysis of Hybrids between *FUCUS SPIRALIS* and *FUCUS VESICULOSUS*

Five characters were considered as readily ascertainable and were used in the separation of *F. spiralis* and *F. vesiculosus*: (i) Vesiculation of the thallus. (ii) Spiral twisting of the thallus. (iii) Receptacle shape. (iv) Presence or absence of a sterile rim to the receptacle. (v) Hermaphrodite or dioecious condition of the receptacle.

Of these characters, nos. (i) and (v) were considered as of more importance than the others and were more heavily weighted accordingly.

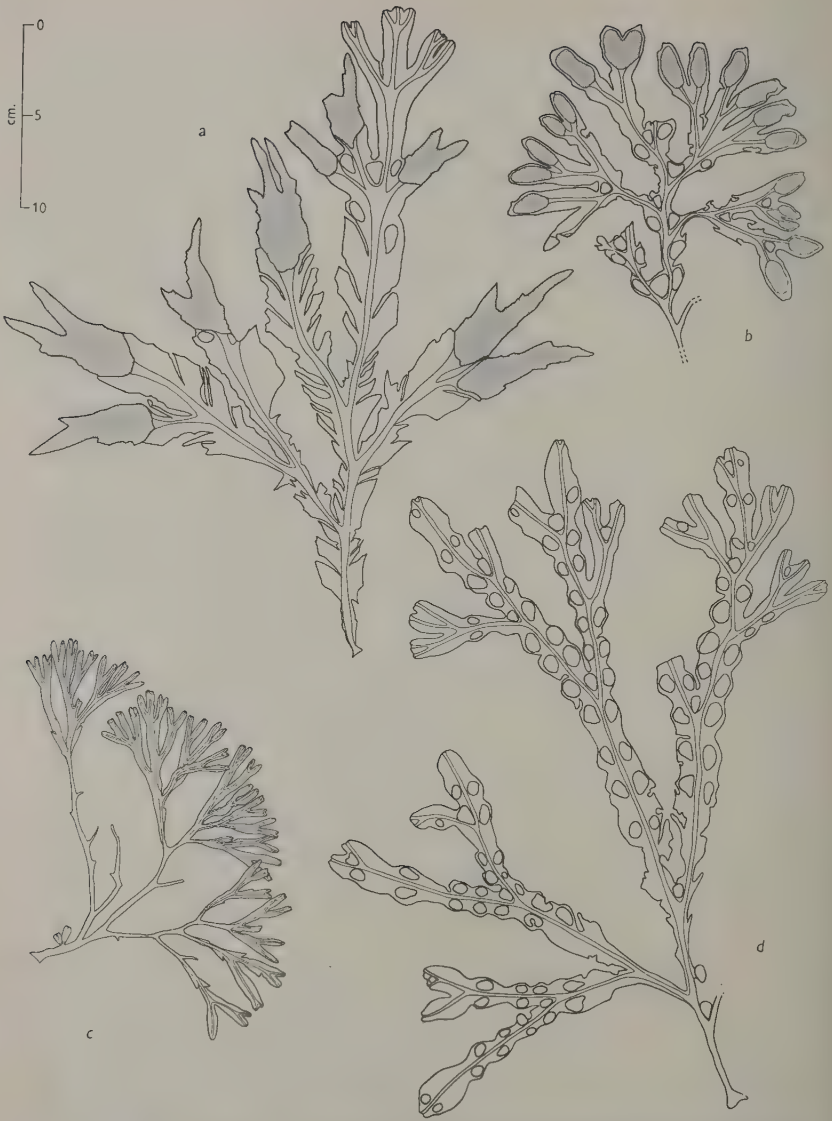

Fig. 3. *a*, *Fucus vesiculosus* × *F. serratus* hybrid, from the experimental strip, Port St Mary, Isle of Man. *b*, *F. spiralis* × *F. vesiculosus* hybrid, with vesicles and rimmed receptacles, from Isle of Man. *c*, *F. vesiculosus* var. *evesiculosus* Cotton, from the outer side of the breakwater, Port Erin, Isle of Man. *d*, *F. vesiculosus* var. *vadorum* Aresch., from Derby Haven, Isle of Man.

Before characters can be used in a hybrid analysis it is necessary to examine the degree of variability in respect of each character shown by the parent species, because on this depends its reliability. Both species show extensive variation in relation to a number of characters and, for *F. vesiculosus* especially, a large number of varieties have been described.

### *Vesiculation of the Thallus as a Diagnostic Character*

Of the two characters, nos. (i) and (v) considered as of greatest importance in separating *F. spiralis* and *F. vesiculosus*, that of the hermaphrodite or dioecious condition is probably the most reliable. It may, as Stomps suggests, be the only one. There is little, if any, evidence that it is a character affected by changes in environmental conditions. Vesiculation of the thallus would appear, however, to be profoundly affected by such changes, and must therefore be considered in some detail. It appears certain from an examination of plants of *F. vesiculosus* found growing under varying degrees of exposure to severe wave action on the south coast of the Isle of Man, that the formation of vesicles is directly correlated with the roughness of the water washing them during the intertidal period. On very exposed areas, such as the outer side of the Breakwater at Port Erin, and at the extreme end of the Langness Peninsula, vesicles are almost entirely lacking. Fig. 3*c* illustrates a typical plant from the former situation, which is probably to be identified as *F. vesiculosus* var. *evesiculosus* Cotton. With increased shelter from the direct breaking force of heavy waves (and quite a small boulder effectively placed will suffice to provide it), vesicles appear and increase in numbers, becoming well developed in quiet waters. The extreme form is that distinguished as var. *vadorum* Aresch. which has rows of closely placed pairs of vesicles and which only occurs in the quietest inlets (Fig. 3*d*). The variation in form and behaviour of *F. vesiculosus* under varying degrees of exposure will be discussed in a separate paper: here it suffices to record merely the distribution of vesiculate and evesiculate plants in relation to degrees of exposure. Similar distributions have been described by Kylin (1907) for the west coast of Sweden, by Cotton (1912, pp. 23–6) for Clare Island, by Richard (1925) for an area on the coast of Belgium, and by Knight & Parke (1950) for the Devon, Manx and Argyll coasts. It is difficult to understand the distribution described for the Argyll coast by Moss (1948), who maintains that with increase in exposure the numbers and sizes of vesicles for *F. vesiculosus* increase. Moss, however, defines the exposure of the coast in terms only of proximity to the open ocean, ignoring the many other factors which are important for algal populations, as, for example, the steepness of the rock surface, the direction of the slope and the presence or absence of outlying rocks which may take the first force of open sea breakers. It is not yet known whether sporelings from evesiculate plants will produce plants forming vesicles if grown under quieter conditions, but experiments are in progress to elucidate this point. However, on a gently sloping shore such as that of the experimental area at Port St Mary, it may be assumed that over relatively small areas environmental conditions will not vary appreciably. Since a proportion of the plants on the strip are evesiculate (Fig. 4*a*), and grow side by side with vesiculate plants, it may be justifiable to seek a different cause for this variation.

Two possible causes suggest themselves. Either (i) there is an evesiculate variety of *F. vesiculosus* which is independent of environmental conditions, or (ii) the plants are the result of crossing with an evesiculate species. However, as will be shown later, this problem probably resolves itself.

### *Spiral Twisting of the Thallus*

This is another character which might depend on environmental conditions. Salt marsh forms of both *F. spiralis* and *F. vesiculosus* are frequently spirally twisted, and it has been suggested by Baker & Bohling (1916) that this is due to a more rapid growth on the lower side kept moist by continued contact with wet mud, compared with the upper side which may be exposed to drying for many days at a time. *F. spiralis* might tend to become twisted because it normally grows at the highest level on the shore and at neap tides may be exposed for long periods. However, similar considerations apply to this character as to that of vesiculation of the thallus and the presence of both spirally and non-spirally twisted thalli in precisely the same locality suggests a different underlying cause.

### *Receptacle Shape*

Receptacle shape may show considerable variation within a single species and especially is this so for *F. vesiculosus*. The appearance of a receptacle is determined by a number of factors of which the most important is probably the length in relation to the breadth. The breadth of a receptacle is partly determined by the breadth of the vegetative frond, and this may be influenced by environmental conditions. With narrowing of the frond, such as occurs with increase in exposure of the plant to severe wave action, the receptacle also becomes narrow until ultimately, on very exposed shores, it becomes completely cylindrical on inflation. Dichotomy of the receptacle is uncommon in *F. spiralis*, whereas in *F. vesiculosus* it may occur once or twice in each receptacle. The degree of inflation of the receptacle may also affect its appearance and this is accentuated in the presence of water of reduced salinity. Fucoids growing at the mouths of rivers or lying in trickles of fresh water running over the shore, have very large swollen receptacles. Thus for *F. vesiculosus* the ellipsoidal or ovate form usually found on sheltered coasts may become more or less cylindrical with increase in exposure, or enlarged by intake of fresh water under conditions of reduced salinity. It is, nevertheless, readily distinguishable from the rounded form of *F. spiralis* with its very conspicuous conceptacles. A population of *F. vesiculosus* was, however, found in the Isle of

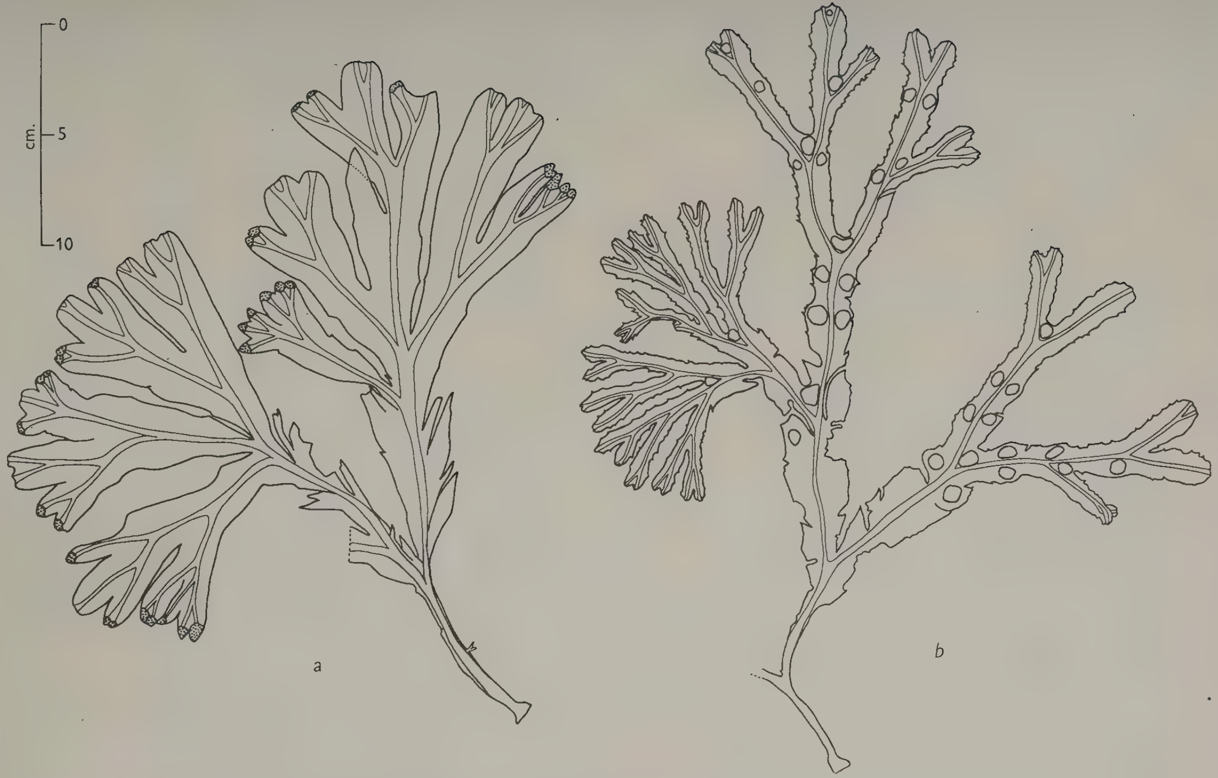

Fig. 4. *a*, an evesiculate plant from the experimental strip, Port St Mary, Isle of Man: *Fucus spiralis* × *F. vesiculosus* hybrid (?). *b*, plant of *Fucus* with vesicles and a serrated edge from a Lundy Island population.

Man in one locality only, which had uniformly rounded receptacles, the plants corresponding to the description of *F. vesiculosus* L. var. *sphaerocarpus* J. G. Agardh. This population was found in a wide shallow depression on the upper part of the shore at Poyll Vaaish several miles distant from the experimental area and it seems unlikely that it would play any appreciable part in the establishment of the strip population. In using receptacle shape as a criterion in separating *F. spiralis* and *F. vesiculosus* there is to be considered the possibility of hybridization with *Ascophyllum nodosum* which also has somewhat rounded receptacles. Especially is this so in view of the fact that Williams (1899) obtained 50% development of hybrid sporelings using eggs of *Fucus vesiculosus* with antherozoids of *Ascophyllum*, and a plant was recorded as occurring in the Menai Straits with external characters intermediate between *Ascophyllum* and *Fucus vesiculosus*. Although this possibility was considered, it was not taken into account in the present discussion because there were no real indications that *Ascophyllum* had played any part in the formation of the strip vegetation. Even though conditions on the strip would now appear to be suitable for the settlement of *Ascophyllum* sporelings, none have yet appeared.

## RESULTS OF ANALYSIS OF HYBRIDS BETWEEN *FUCUS VESICULOSUS* AND *FUCUS SPIRALIS*

Fig. 5 shows the results of the hybrid analysis between *F. vesiculosus* and *F. spiralis* for four samples from the strip vegetation taken from different tide levels. The uppermost sample was taken from M.H.W.N.T. and the lowest from a little below M.S.L. The diagrams show percentage frequency distributions for plants with index numbers ranging from 0 (pure *F. spiralis*) to 14 (pure *F. vesiculosus*) The fifth histogram summarizes the distributions for the whole population. The pattern of the distribution is similar for the three upper samples: about 20% of *F. spiralis*, somewhat less than this of *F. vesiculosus*, and a range of intermediate forms between. In the lowest sample there is a marked decrease in the proportion of *F. spiralis* and an increase in that of *F. vesiculosus*. The large percentage of plants with an index number of 10 is due largely, but not entirely, to the presence of plants similar to *F. vesiculosus* in all respects except that they lacked vesicles. It is possible that these represent a genetically distinct variety but only cultural experiments could decide this point.

The gametes from the intermediate forms were fully formed and active.

## FORMS INTERMEDIATE BETWEEN *FUCUS VESICULOSUS* AND *FUCUS SERRATUS*

One great difficulty preventing the completion of hybrid diagrams for *F. vesiculosus* and *F. serratus* is the fact that although the fruiting periods of the two species overlap to some extent, they are not sufficiently coincident; only

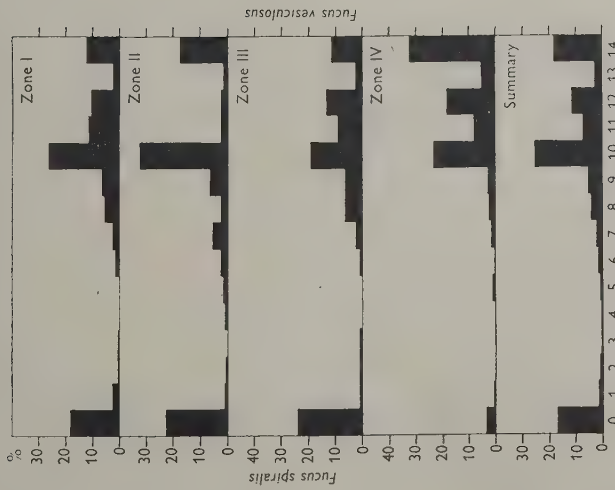

Fig. 5. Hybrid diagrams from Port St Mary *Fucus* population.

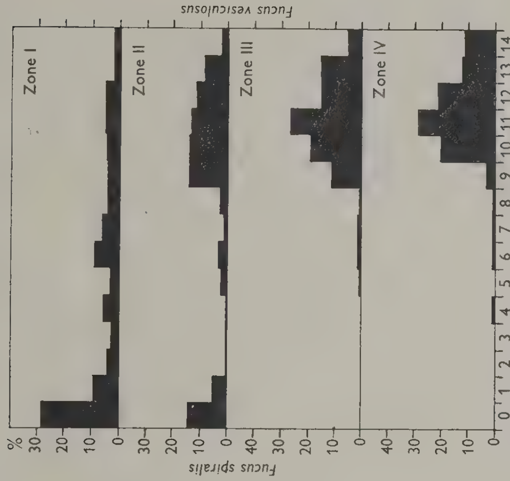

Fig. 6. Hybrid diagrams of River Mersey *Fucus* population.

when all the plants are in the fruiting condition can the necessary distinctions be made. Plants intermediate between *F. vesiculosus* and *F. serratus* were found on the strip in the fruiting condition when *F. vesiculosus* was in fruit. This indicates either that the reproductive period of the hybrids extends over that of both parents, or that the period for some hybrids is coincident with that of *F. vesiculosus* while for others it may be coincident with that of *F. serratus*. Hybrids between *F. vesiculosus* and *F. serratus* were not as common as those between *F. vesiculosus* and *F. spiralis*, the fruiting periods of which overlap much more completely than those of the former pair of species.

## The Occurrence of Hybrids under Natural Conditions

The strip at Port St Mary was a highly artificial area; an experiment of similar extent is unlikely to occur in nature and, as Anderson (1936) remarks, 'Hybridization is much more frequent in areas greatly disturbed by man than under natural conditions'. The question therefore arises as to whether, and if so how frequently, hybrids occur naturally. There is no doubt that hybrids among the three species of *Fucus* occur quite frequently on the open shore; many more have been found by the present authors since their existence has been recognized than had been previously noticed. Kniep (1925) suggested that the most favourable position for hybrids would be in the regions between the more sharply defined zones of the parent species, and it is in such regions that the majority of natural hybrids have been found on the Manx coasts. For example, plants with characters intermediate between those of *F. vesiculosus* and *F. serratus* occur frequently on the gently sloping rocks on the lower part of the Poyll Vaaish shore where the population is sparse and in a position in which the *F. vesiculosus* and *F. serratus* zones overlap. It is likely that the evesiculate plants mixed with *F. spiralis* in the upper part of the shore that are described by Knight & Parke (1950) as *F. vesiculosus* var. *evesiculosus* Cotton and evesiculate by virtue of their high position on the shore, are hybrids between *F. vesiculosus* and *F. spiralis*. Present observations do not support the suggestion that there is a relation between vesiculation and vertical distribution on the shore.

## A Hybrid Population on the River Mersey Shore

A second 'hybrid swarm' population has been found occurring naturally on the south bank of the River Mersey about 4 miles from Liverpool. Probably its presence in this region is due ultimately to the nature of the rock surface which is of very soft sandstone and can support only a limited size and weight of plant. Once the plants exceed a certain weight, the rock surface flakes away leaving a bare area open to recolonization. Thus the community is an open one and competition not as intense as it is on a firm rock surface. In addition, the fruiting period of *Fucus spiralis* is longer here and considerably overlaps that of *F. vesiculosus*. There is no period of the year at which plants cannot be found in the full fruiting condition, though possibly the extended fruiting period is more characteristic of the hybrids than of the parent species. Fig. 6 shows hybrid analyses for *F. spiralis* and *F. vesiculosus* from square metres of algal vegetation, for four positions on the shore ranging from the region of high water down to about M.S.L. The fucoid vegetation exists as a continuous cover only in the upper part of the shore. Lower down the population is scattered and consists only of short stunted plants. The water covering the plants at high tide is so muddy that the bulk of assimilation must be carried out at low tide when the plants are exposed and the degree of exposure at M.S.L. probably represents the minimum exposure to light required for effective assimilation (Burrows, 1947). The Mersey community is not a new one and the plants show a distinct zonation. *F. spiralis* is limited to the top of the shore as are also the hybrids approaching *F. spiralis*. Lower down only the hybrids approaching *F. vesiculosus* persist. An interesting feature of the population is that the hybrids are much more common than the parent species. It would appear that a hybrid approaching *F. vesiculosus* and not the parent species is best adapted to the conditions prevailing here. There were also other features of interest. All the plants which were evesiculate and dioecious were male. Many of the apparent hybrid plants had no vegetative apices: all had formed receptacles and so set a limit to the life of the plant. Probably on the fall of the receptacles new frondage would arise by proliferation, this condition being characteristic of many of the plants in this locality.

Stomps (1911) found at Nieuport on the coast of Belgium, where the Chenal de L'Yser runs into the sea, a series of forms of *F. vesiculosus* and *F. spiralis* connecting the two species apparently precisely like the series on the River Mersey. He considered the question of the origin of these forms and ruled out hybridization on the basis of their distribution in his area. He remarked that our knowledge is still so limited that we cannot disregard *a priori* the possibility that the irregularities found on the shore may be due to hybridization, but he could not understand, if these aberrant individuals could so be explained, why they were more numerous in the canal region than on the sea coast.

Possibly here, as also on the River Mersey, their presence may be due to the open nature of the community. The evidence accumulated in this present investigation supports the view that such forms occur on the open coast under conditions of less acute competition from fully grown plants of the parent species, and supports Kniep's suggestion that it is this competition which prevents the establishment of hybrid plants in a fully developed open-shore zonation.

Stomps concluded from his observations that there is only one species of *Fucus* in place of the three, *spiralis*, *vesiculosus* and *ceranoides* (which he included), these being apparently habitat forms of a single species, environmental conditions deciding which hereditary characters shall be manifested in any one locality. Since over a large part of the rocky coast of Britain the characteristic fucoid vegetation is developed and in it the three taxonomic species remain distinct, there can be no advantage in disregarding this conception of them, i.e. as taxonomic species. Since up to the present it has not been possible to carry out cultural experiments on fucoids, mainly because of the difficulties of imitating intertidal conditions, the determination of the exact status of the three species must be assessed on somewhat circumstantial evidence. The results of the ecological experiment described have shown that there is no inherent sterility barrier among the three taxonomic species. This may also be true for other species of *Fucus* as, for example, *F. ceranoides* L., since hybrids between this species and *F. spiralis* have been reported (Sauvageau, 1908; Gard, 1910). Nothing has been found to run counter to the suggestion of Kniep (1925) that competition with the parent species prevents the development of hybrid plants in nature. Thus the barrier to complete merging of the species into one polymorphic species appears to be an ecological one, and it would appear that they are becoming isolated within specific tidal limits under the conditions prevailing in well-established open-shore vegetation. On the shore great changes in ecological conditions occur over relatively limited areas. A difference of 1 ft. in tide-level in the intertidal region of the shore may be equivalent to a large change in environmental conditions in terms of exposure to a drying atmosphere, changing light intensities, temperatures and the influence of water of variable salinity. It is likely that continued isolation in different parts of the intertidal region will ultimately lead to the development of other barriers, e.g. those of intersterility.

Using the ecotype terminology it would be difficult to know whether to regard these taxonomic species as ecotypes or ecospecies, since hybrid swarm populations may occur between them in nature, although, as far as we know, only rarely. The condition appears to be somewhat similar to that found for species of *Silene* among flowering plants from work carried out by Turrill and Marsden-Jones and reported by Turrill (1938). In north-west Europe ecological barriers alone keep them as distinct taxonomic units, and occasional hybrid swarm populations are found in nature.

Variation within the *Fucus* species may also occur along ecological gradients, one of which has been described, but many more probably exist, e.g. gradients of tidal depths, and reduction of the salinity of the water. Other types of variation also occur within the species which it is more difficult to connect with changes in environmental conditions. Whole populations may possibly be of hybrid origin. There has recently been found at Lough Ine in the West of Ireland a population showing the texture and serration of *F. serratus*, the spiral twisting and rounded and rimmed receptacles of *F. spiralis* and with somewhat irregular vesicular inflations. Similarly, a population exists on Lundy Island where plants possessing the vesicles of *F. vesiculosus* have serrated fronds characteristic of *F. serratus* (Fig. 4*b*). Species problems of this kind will probably arise for many different algae when more is known of their autecology and cytogenetical relationships.

## ACKNOWLEDGEMENTS

We are indebted to Prof. J. H. Orton, F.R.S., and Mr N. S. Jones, who initiated the cleared-strip experiment, for permission to sample the resulting population. We also wish to thank Dr Margery Knight and Dr Mary Parke for reading the manuscript, and Mr R. B. Burrows whose co-operation made the work possible. Dr Parke kindly sent the material from Lundy Island.

## SUMMARY

Characters used to distinguish *Fucus spiralis* L., *F. vesiculosus* L. and *F. serratus* L. are listed. Cross-fertilization between pairs of these species has been observed—independently by several workers.

Ecological habitats of the three species are described and the influence of competition on zonation is indicated. A *Fucus* population occurred on an area cleared of limpets at Port St Mary, Isle of Man, in which the majority of plants could not definitely be assigned to any one *Fucus* species.

Anderson's method of hybrid analysis was applied to samples from various levels on the area. The characters used in the analysis are listed and their status briefly discussed.

A direct relationship is recorded between vesiculation of the thallus of *F. vesiculosus* and the degree of exposure of the habitat to severe wave action. The extreme form for very sheltered localities is *F. vesiculosus* var. *vadorum* Aresch. and for exposed situations, *F. vesiculosus* var. *evesiculosus* Cotton. Great range in vesiculation in adjacent plants on the experimental strip is therefore due to hybridity or to a varietal form of *F. vesiculosus*.

Spiral torsion of the thallus in relation to environmental conditions is discussed.

Variation in receptacle shape in *F. vesiculosus* and *F. spiralis* is considerable; nevertheless, the use of this character in the hybrid analysis is justified.

Hybrid analysis between *F. vesiculosus* and *F. serratus* is difficult to carry out owing to the non-coincidence of fruiting periods of the parent plants.

The occurrence of hybrids in undisturbed populations in the Isle of Man is recorded.

A 'hybrid swarm' population by the River Mersey has been analysed and its significance discussed. An attempt has been made to assess the present status of the three species of *Fucus*.

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# LITTORAL DIATOMS FROM THE SALSTONE, NEAR PLYMOUTH

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and the Plymouth Laboratory

(Text-figs. 1, 2)

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## INTRODUCTION

The diatom flora inhabiting the muddy shores and bottoms off Plymouth has received little attention in comparison with the fauna associated with such muds. Since a large number of the microfauna depend, to a great extent, upon the diatoms as a source of food (Mare, 1942), a knowledge of the latter is therefore desirable.

The present paper is mainly concerned with the diatoms inhabiting the mud-flats at the Salstone, a small island lying in the Salcombe estuary about one and a half miles above Salcombe. The habitat is of particular interest since it is sheltered from wave action, well defined, and hardly disturbed by man. Marine conditions prevail, the small fresh-water streams seeming to exert no appreciable influence on the salinity. Very few species of diatoms belonging to fresh water have been met with during the analysis of the present samples, and since these were in negligible quantities, they are excluded from the list given below.

The tidal range at the Salstone is of the order of 15 ft., but the islet itself lies well below M.H.W.S.; its uppermost parts being covered with *Ascophyllum nodosum*. The fucoids growing on this islet, as well as on the rocky shores facing it, display the usual zonation; a more detailed account of these will be dealt with separately by one of us (A. A. A.).

The diatoms considered below have been collected by the latter author during the months of February and March 1949, mainly from the mud-flats surrounding the islet, where a *Vaucheria* community covers large areas of the flats and extends to a level below M.L.W.S. The *Vaucheria* community harbours a large number of diatoms, some of which were found in abundance at the time of collection. The analysis of the samples has been carried out by us together at Plön.

Among the immense number of papers about diatoms, there are only very few specially dealing with the marine littoral vegetation. The most exhaustive one is written by Hustedt (1939) about the German coast of the North Sea. On British shores, Ghazzawi (1933) made a short study of the littoral diatoms of the Liverpool and Port Erin shores. He enumerates ninety-four species and varieties, but ten of these species are fresh-water diatoms which do not really belong to the marine flora and therefore are not mentioned in our list. Of the remaining eighty-four species, forty-three were not found in our samples, or at least not recognized with certainty, though we are convinced that further studies in the Plymouth region will considerably increase the number of species upon our mud-flats.

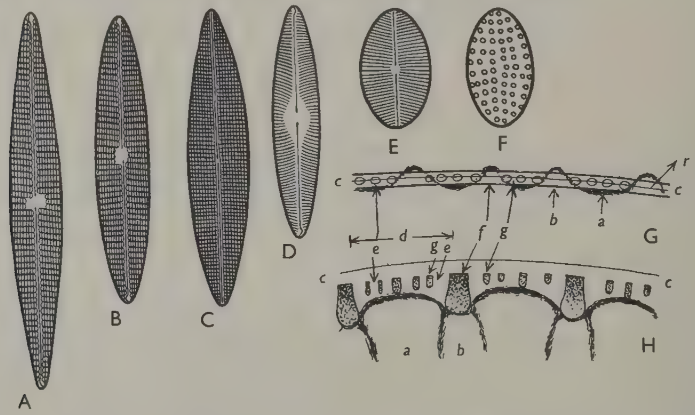

Fig. 1. A, B, *Navicula ramosissima* Ag. × 1200. C, *N. britannica,* n.sp. × 1200. D, *N. aleemi* n.sp. × 1200. E, F, *Cocconeis guttata,* n.sp. × 1200. G, part of the ale of *Surirella striatula* Turp., top view. × 1200. H, the same, seen from the inner side of the valve. × 1200. *a,* crests; *b,* furrows; *c,* alar border canal; *d,* primary canal; *e,* secondary canals; *f,* primary windows; *g,* secondary windows; *r,* slit of the raphe. F.H. ad nat. del.

## SYSTEMATIC ACCOUNT OF THE SPECIES

For the identification of the species the diatom material was boiled in acid in the usual way to get rid of the organic content of the cells, and subsequently thoroughly washed, the clean frustules being mounted in hyrax. The taxonomic arrangement followed is that of Hustedt (1930*a*).

### Genus **Melosira** Ag.

*Melosira moniliformis* (Müll.) Ag. (Hustedt, 1930*b*, p. 231, fig. 95). Rather rare. The density of this species in certain localities on the southern coast of

England shows considerable variation between the seasons as well as between different years (Aleem, 1950*b*).

*M. Westii* W.Sm. (Hustedt, 1930*b*, p. 268, fig. 113). Rather frequent at M.T.L. and M.L.W.S. Occurs separately or in colonies of a few individuals. Longer chains were not met with.

*M. sulcata* (Ehr.) Kütz. (Hustedt, 1930*b*, p. 276, fig. 119). Much more frequent than the other two species. It is a cosmopolitan diatom of general distribution, also known among the plankton as well as among littoral marine sediments, both recent and fossil.

### Genus **Podosira** Ehr.

*Podosira Montagnei* Kütz. (Hustedt, 1930*b*, p. 281, fig. 122). Rare: a few valves were met with in samples from the *Vaucheria* community. This species is more common on rocky shores.

*P. stelliger* (Bail.) Mann (Hustedt, 1930*b*, p. 286, fig. 128). This form grows attached to algae on rocky shores. Its presence on the mud-flats is probably due to sedimentation from the plankton.

### Genus **Hyalodiscus** Ehr.

*Hyalodiscus scoticus* (Kütz.) Grun. (Hustedt, 1930*b*, p. 293, fig. 133). Rare, probably also sedimented from plankton.

### Genus **Sceletonema** Grev.

*Sceletonema costatum* (Grev.) Cleve (Hustedt, 1930*b*, p. 311, fig. 149). Rare, sedimented from plankton.

### Genus **Thalassiosira** Cleve

*Thalassiosira decipiens* (Grun.) Joerg. (Hustedt, 1930*b*, p. 322, fig. 158). Rather rare; valves both of resting spores (thick-walled with coarse structure) and of vegetative cells (thinner walls) were found. Sedimented from plankton, more frequent in offshore waters near Plymouth in February–March.

### Genus **Coscinodiscus** Ehr.

The species of *Coscinodiscus* found on the mud-flats at the Salstone are all planktonic.

*C. excentricus* Ehr. (Hustedt, 1930*b*, p. 400, fig. 211). Frequent. This species is widely distributed in all mud sediments on the north Atlantic coasts, especially in Germany and the Norwegian fjords.

*C. radiatus* Ehr. (Hustedt, 1930*b*, p. 420, fig. 225). Rare.

*C. centralis* Ehr. (Hustedt, 1930*b*, p. 444, fig. 243). Only fragments were found.

### Genus **Roperia** Grun.

*Roperia tessellata* (Roper) Grun. (Hustedt, 1930*b*, p. 523, fig. 297). Rare, deposited from plankton.

### Genus **Actinoptychus** Ehr.

*Actinoptychus undulatus* (Bail.) Ralfs (Hustedt, 1930*b*, p. 475, fig. 264). Rather frequent. Only specimens of small size have, however, been encountered. The species is pelagic, though frequently met with in marine sediments.

### Genus **Eucampia** Ehr.

*Eucampia zoodiacus* Ehr. (Hustedt, 1930*b*, p. 772, fig. 451). Only a few valves found. Planktonic.

### Genus **Triceratium** Ehr.

*Triceratium alternans* Bail. (Hustedt, 1930*b*, p. 825, fig. 488). Rare, also found in colonies attached to the algae on rocky shores as well as being pelagic.

### Genus **Biddulphia** Gray

*Biddulphia aurita* (Lyngb.) Bréb. & God. (Hustedt, 1930*b*, p. 846, fig. 501). Rather rare at the Salstone. It was much more frequent on the mud-flats at Whitstable, Kent (Aleem, 1950*a*). This species, which also occurs in a pelagic form, was produced in enormous quantities in the littoral region at Swanage, Dorset, during the spring of 1947 following a cold and rather long winter, while at the same period in the following year it was much less abundant (Aleem, 1950*b*). Hustedt (1939) found this species in almost all samples collected from the mud-flats on the northern coasts of Germany. The species seems not to be endemic in the mud-flats but rather deposited there.

### Genus **Rhabdonema** Kütz.

*Rhabdonema minutum* Kütz. (Hustedt, 1931, p. 18, fig. 548). Abundant in the *Vaucheria* community, less frequent on bare mud.

*Rh. arcuatum* (Lyngb.? Ag.) Kütz. (Hustedt, 1931, p. 20, fig. 549). Rather rare in the *Vaucheria* community.

### Genus **Striatella** Ag.

*Striatella unipunctata* (Lyngb.) Ag. (Hustedt, 1931, p. 32, fig. 560). Rather rare in the *Vaucheria* community.

### Genus **Grammatophora** Ehr.

*Grammatophora marina* (Lyngb.) Kütz. (Hustedt, 1931, p. 43, fig. 569). Not infrequent among the *Vaucheria* community, rather rare on bare mud.

*G. serpentina* (Ralfs) Ehr. (Hustedt, 1931, p. 49, fig. 577). Very rare, found only among the *Vaucheria* community.

### Genus **Licmophora** Ag.

The species belonging to this genus were more frequent in the *Vaucheria* community than on bare mud. The intercalary bands of the cells can be taken as a good character to distinguish the species. The septa in these bands are very short in *Licmophora flabellata* and *L. Juergensi*, a little more distinct in *L. gracilis* and *L. hyalina*, while they are very deep in *L. Ehrenbergi* and *L. paradoxa*.

*L. flabellata* (Carm.) Ag. (Hustedt, 1931, p. 58, fig. 581). Abundant, easily distinguished from the others by its four plate-like chromatophores.

*L. gracilis* (Ehr.) Grun. var. *anglica* (Kütz.) Peragallo (Hustedt, 1931, p. 60, fig. 583). Rather rare.

*L. Juergensi* Ag. (Hustedt, 1931, p. 63, fig. 586). Rather common. Longitudinal and transverse striae of the valve are distinct.

*L. Ehrenbergi* (Kütz.) Grun. (Hustedt, 1931, p. 70, fig. 593). Rare, distinguished by its large size and coarse striae which are slightly radiate at the apex of the valve.

*L. paradoxa* (Lyngb.) Ag. (Hustedt, 1931, p. 76, fig. 605). Very common, especially in the *Vaucheria* community.

*L. hyalina* (Kütz.) Grun. (Hustedt, 1931, p. 81, fig. 611). Rather frequent. The shape of the valve resembles that of a tennis-racket with a short handle. The striae are dense (about 30 in 10 $\mu$), they are to be distinguished only on the lower part of the valve, while the upper part appears hyaline.

### Genus **Dimerogramma** Ralfs

*Dimerogramma minor* (Greg.) Ralfs (Hustedt, 1931, p. 118, fig. 640). Not uncommon.

### Genus **Opephora** Petit

*Opephora marina* (Greg.) Petit (Hustedt, 1931, p. 136, fig. 656). Not infrequent in the *Vaucheria* community.

### Genus **Rhaphoneis** Ehr.

*Rhaphoneis surirella* (Ehr.) Grun. (Hustedt, 1931, p. 173, fig. 679*a–c*). Rather common. Widely distributed in all mud-flats.

*R. amphiceros* Ehr. (Hustedt, 1931, p. 174, fig. 680). Frequent, the valves in this species differ considerably both in size and shape.

### Genus **Synedra** Ehr.

*Synedra Gailloni* (Bory) Ehr. (Hustedt, 1931, p. 195, fig. 690). Rather frequent.

*S. tabulata* (Ag.) Kütz. (Hustedt, 1931, p. 218, fig. 710*a–d*). Common.

var. *fasciculata* (Kütz.) Grun. (Hustedt, 1931, fig. 710*i–l*). Frequent. The cells in this variety tend to grow attached together in colonies like those of *Fragilaria*.

var. *acuminata* Grun. (Hustedt, 1931, p. 219, fig. 710*e, f*). Not infrequent, distinguished by its long, protracted, rostrate ends.

*Synedra crystallina* (Ag.) Kütz. (Hustedt, 1931, p. 232, fig. 719). Rather rare.

*S. investiens* W.Sm. (Hustedt, 1931, p. 209, fig. 699). Rare.

### Genus **Thalassionema** Grun.

*Thalassionema nitzschioides* Grun. (Hustedt, 1931, p. 244, fig. 725). Rare, sedimented from the plankton.

### Genus **Thalassiothrix** Cleve & Grun.

*Thalassiothrix longissima* Cleve & Grun. (Hustedt, 1931, p. 247, fig. 726). Very rare. Deposited from plankton. The species is easily distinguished by its very long and narrow valves with spiny edges.

### Genus **Campyloneis** Grun.

*Campyloneis Grevillei* (W.Sm.) Grun. (Hustedt, 1931, p. 321, fig. 781). Rare, more frequent on rocky shores, where it grows attached to algae such as *Polysiphonia* and *Cladophora*.

### Genus **Cocconeis** Ehr.

*Cocconeis scutellum* Ehr. (Hustedt, 1931, p. 337, fig. 790). Very common, especially in the *Vaucheria* community.

var. *stauroneiformis* W.Sm. (Hustedt, 1931, p. 339, fig. 792). Frequent. The central area of the raphe-valve is enlarged into a narrow band reaching the margin.

*C. dirupta* Greg. (Hustedt, 1931, p. 354, fig. 809). Not infrequent in the *Vaucheria* community.

*C. pelta* A. Schmidt (Hustedt, 1931, p. 361, fig. 815). Rare. This species is similar to another species, namely *C. peltoides* Hustedt (1939, p. 606, figs. 23–27), which is more frequent in the mud-flats of the German coast. The latter, however, can be easily distinguished by the absence of a clear median area which is very distinct and punctate in *C. pelta* A.S.

*C. guttata* **sp.nov.** Valva elliptica, 15 μ longa, 9 μ lata. Raphovalva raphi directa, area axiali angusta, area centrali parva, striis radiantibus, circiter 22 in 10 μ. Areovalva area longitudinali angusta, granulata, granulis in lineis radialibus dispositis, circiter 9 in 10 μ (Fig. 1 E, F).

Valves elliptical, length about 15 μ, breadth about 9 μ. Raphe-valve with straight raphe, axial-area narrow, central-area rounded, very small, striae dense, about 22 in 10 μ, distinctly radiate, indistinctly punctate. Rapheless valve with rather narrow pseudoraphe, somewhat irregular, coarsely dotted; dots in slightly radiate rows, 8–9 in 10 μ.

*C. guttata* resembles *C. distans* Greg. in shape and structure of the valves. The striae in the former are much denser, however, being almost twice as dense. Besides, in *C. distans* the puncta are included in transapical costae which are slightly inflated round each punctum (Hustedt, 1931, p. 344, fig. 797. Peragallo, 1897–1908, pl. 3, figs. 17, 18). Such costae do not exist in our species where the large dots are distinctly separated from each other. Nevertheless, further investigations may be required to decide whether these differences are constant.

*C. guttata* is very rare on the mud-flats at the Salstone. Type specimen preserved in the collection of Fr. Hustedt.

### Genus **Achnanthes** Bory.

*Achnanthes Lilljeborgei* Grun. (Hustedt, 1939, p. 609, figs. 39, 40). Very rare. The discovery of a single complete frustule of this characteristic species in our samples from the Salstone flats is very interesting since it sheds further light on our knowledge of this species. Length about 28 μ, breadth 8 μ, rapheless valve with faintly punctate costae, 9 in 10 μ. The raphe-valve is thinner, with denser striae, 15 in 10 μ, which are almost perpendicular to the median line. Raphe straight, axial area very narrow, no central area.

This is perhaps the second time in which the two real valves which belong to this species have been found together, the first was by Hustedt (1939) from the mud flats on the German coast. The specimens from these two localities are identical.

The rapheless valve of this species as figured by Cleve (1892, pl. 3, fig. 19) and Peragallo (1897–1908, pl. 2, fig. 5, right fig.!) is so characteristic that the specimen found by us undoubtedly belongs to this species. On the other hand, the valve with raphe which has been drawn both by Cleve (fig. 20) and by Peragallo (fig. 5, left fig.!) apparently do not belong to this species, as has been pointed out by Hustedt (1939), but rather to *Navicula palpebralis* f. *Vahliana* (Grun.) Hust., which seems to be generally distributed on mud-flats in the European north Atlantic coasts. The statement by Cleve (1895) that the axial area of the lower (=raphe-) valve of *Achnanthes Lilljeborgei* is 'lanceolate narrow' applies more to this *Navicula*.

There can be no doubt that the raphe-valve which we found attached to the rapheless valve in our material is the true valve of this *Achnanthes*.

*A. Hauckiana* Grun. (Hustedt, 1931, p. 388, fig. 834). Rare. Brackish water species of general distribution on European coasts.

*A. brevipes* Ag. (Hustedt, 1931, p. 424, fig. 877*a–c*). Only a few valves were met with in the sediment.

var. *parvula* (Kütz.) Cleve (Hustedt, 1931, p. 426, fig. 877*f–i*). Rare. Both the species and its variety are more common on rocky shores in the spray zone (Aleem, 1950*b*).

*A. longipes* Ag. (Hustedt, 1931, p. 427, fig. 878). Very common in the *Vaucheria* community in the lower littoral region. The zonal distribution of this species at the Salstone is similar to that described by Aleem (1950*b*) from other localities.

### Genus **Diploneis** Ehr.

*Diploneis bombus* Ehr. (Hustedt, 1931, p. 704, fig. 1086). Rather rare.

*D. aestuari* Hustedt, (Hustedt, 1939, p. 612, figs. 41, 42). Rather frequent, first known from the German coast. Valve elliptical, slightly constricted, length about 15 μ, breadth about 6 μ, transapical striae about 18 in 10 μ.

### Genus **Amphipleura** Kütz.

*Amphipleura rutilans* (Trent.) Cleve (Hustedt, 1931, p. 720, fig. 1093 *a*, *b*). Frequent, filaments were found growing on the mud at M.T.L.

### Genus **Stauroneis** Ehr.

*Stauroneis salina* W. Smith (Hustedt, 1930 *a*, p. 258, fig. 414). Frequent, the species has a wide distribution in the mud-flats.

### Genus **Navicula** Bory.

Since only a comparatively small number of species of this very large genus were found, we prefer to give them here in alphabetical order.

*Navicula abrupta* Greg. (Cleve, 1895, p. 61, A.S. Atl. pl. 3, figs. 1, 2). Frequent, some of the specimens found are smaller than is cited in the literature. The smallest valves found are about 30 μ long and 17 μ broad.

*N. aleemi* Hustedt, **sp.nov.** Valva lineari-lanceolata, apicibus subobtusis, non protractis, circiter 26 μ longa et 6 μ lata. Raphe directa, area axiali angusta, in media parte valvarum lanceolate amplificata, area centrali modice lata. Striis in media parte valvarum leniter radiantibus, 20–24 in 10 μ, ad polos leniter convergentibus, densioribus, circiter 30 in 10 μ (Fig. 1 D).

Valve linear-lanceolate with slightly convex margins and rather obtusely rounded ends, about 26 μ long and 6 μ broad. Raphe straight, embedded in a distinct longitudinal median rib. Axial area narrow, towards the central nodule lanceolately enlarged. Central area moderately large, elliptical lanceolate. Striae slightly radiate, at the ends of the valve slightly convergent, round the central area 20–24 in 10 μ, becoming denser towards the ends, till 30 in 10 μ. Longitudinal lines inconspicuous.

This species belongs to the group of the *Naviculae lineolatae*, but is distinguished from the other species by its distinct longitudinal median rib, the shape of the areas and by its dense structure.

Rare, found on the mud flats at the Salstone, type specimen in the collection of Fr. Hustedt.

*N. arenaria* Donk. (Donkin, 1871–2, p. 56, pl. 8, fig. 5). Not rare. More frequent on sandy flats (Hustedt, 1939, p. 622).

*N. avenacea* (Bréb.) (Cleve, 1895, p. 15). Rare, only a few valves belonging to this species have been found.

*N. britannica* **sp.nov.** Valva lineari-lanceolata, apicibus acutis, circiter 39 μ longa et 8 μ lata. Raphe directa, poris centralibus approximatis, area axiali angustissima, area centrali nulla. Striis transapicalibus fere perpendicularibus vel leniter radiantibus, circiter 20 in 10 μ, striis longitudinalibus directis, circiter 24 in 10 μ (Fig. 1 c).

Valves linear-lanceolate with convex margins and acute ends, 39 μ long and 8 μ broad. Raphe straight, with very approximate central pores, axial area very narrow, no central areas. Striae perpendicular to the median line or very slightly radiate, about 20 in 10 μ, crossed by distinct straight longitudinal lines, about 24 in 10 μ.

This species also belongs to the *Naviculae lineolatae*, especially to the group of *N. ramosissima* Ag. and its allied forms. It is distinguished by its very approximate central pores and its denser structure.

Found on the mud-flats of Salstone, but rare. Type specimen in the collection of Fr. Hustedt. The species was also found previously by one of us (A. A. A.) at Swanage.

*N. cancellata* Donk. (Cleve, 1895, p. 30). Frequent, easily recognized by its strong and distinctly lined ribs and slightly constricted frustules in girdle view.

*N. crucigera* (W. Smith) Cleve (Hustedt, 1930*a*, p. 270, fig. 439). Frequent.

*N. cryptocephala* Kütz. (Aleem, 1949, p. 436, fig. 8*a*, *b*). Frequent, widely distributed in mud-flats.

var. *veneta* Kütz. (Aleem, 1949, fig. 8*c*, *d*). Frequent.

*N. digitoradiata* (Greg.) A. Schmidt (Hustedt, 1930*a*, p. 301, fig. 518). Frequent.

*N. flanatica* Grun. (Hustedt, 1939, p. 628, figs. 86–90). Rather frequent, distinguished by its distinct lanceolate axial area and by its coarse longitudinal lines.

*N. forcipata* Grev. (Cleve, 1895, p. 65). Frequent.

var. *densestriata* A. Schmidt, (p. 66). Rather frequent, valves 50–60 μ long, 15 μ broad, striae 22 in 10 μ.

*N. gregaria* Donk. (Hustedt, 1930*a*, p. 269, fig. 437). Frequent, distinguished from *N. cryptocephala* mainly by its less radiate striae and the presence of clear longitudinal lines.

*N.* (*Schizonema*) *grevillei* Ag. (Cleve, 1894, p. 152). Rare.

*N. groschopfi* Hustedt (Hustedt, 1939, p. 631, figs. 102, 103). Frequent, first described by Hustedt from mud-flats on the German coast. The species is characterized by its small size and dense striae (20 in 10 μ) and rhombic-lanceolate valves.

*N. lyra* Ehr. (Cleve, 1895, p. 63). Rare, widely distributed on mud-flats. Most of our specimens belong to var. *intermedia* Peragallo (1897–1908, pl. 23, figs. 6–10), which we have not separated.

*N. ostrearia* Turp. (Peragallo, 1897–1908, pl. 7, fig. 22). Common. This *Navicula* is easily distinguished in the living state by its blue colour and hyaline structure. It grows associated with mussels and shells in the *Fucus* zone.

*N. palpebralis* Bréb. f. *Vahliana* (Grun.) (Hustedt, 1939, p. 635. Schmidt, 1874, pl. 2, fig. 21). Rather frequent, widely distributed on mud-flats.

*N. plicata* Donk. (Cleve, 1894, p. 154). Not frequent. The valves in this species are in most cases linear-lanceolate with more or less convex margins, but not linear alone as described by Cleve, and Peragallo (1897–1908, pl. 8, fig. 15). Besides, the striae are more radial than is shown in Peragallo's figure.

*N.* (*Schizonema*) *ramosissima* Ag. (Cleve, 1894, p. 26). Frequent. (Fig. 1 A, B).

var. *mollis* (W. Smith) (Aleem, 1949, p. 432, fig. 6*f*, *g*). Frequent.

*N. salinicola* Hustedt (Hustedt, 1939, p. 638, figs. 61–69). Frequent.

### Genus **Pinnularia** Ehr.

*Pinnularia ambigua* Cleve (Cleve, 1895, p. 94). Rare. As Hustedt (1939, p. 641) has already pointed out, this species should perhaps be transferred into the genus *Amphora*. The frustules are distinguished by a rather larger number of intercalary bands and are mostly asymmetrical to the apical plane as in the species of the genus *Amphora*. The valves are not always symmetrical to the apical axis, but more or less asymmetrical. We leave this species at present in *Pinnularia* until further studies of these two genera are undertaken.

### Genus **Trachyneis** Cleve

*Trachyneis aspera* (Ehr.) (Cleve, 1894, p. 191). Rare, also known from other mud-flats of the European coasts.

### Genus **Scoliopleura** Grun.

*Scoliopleura tumida* (Bréb.) Rabh. (Heiden in Schmidt (1874–1944), pl. 262, figs. 1–4, 6). Frequent.

### Genus **Scoliotropis** Cleve

*Scoliotropis latestriata* (Bréb.) Cleve (Heiden in Schmidt (1874–1944), pl. 261, figs. 4, 5). Rather frequent.

### Genus **Caloneis** Cleve

*Caloneis liber* (W. Smith) (Cleve, 1894, p. 54). Rare.

### Genus **Gyrosigma** Hass.

*Gyrosigma balticum* (Ehr.) Rabh. (Hustedt, 1930*a*, p. 224, fig. 331). Not infrequent, easily distinguished by its more or less long linear valves and distinct striae.

*G. Spenceri* (W. Smith) Cleve (Hustedt, 1930*a*, p. 225, fig. 336). Rather frequent.

*G. fasciola* (Ehr.) (Cleve, 1894, p. 116). Frequent, characterized by its long protracted ends.

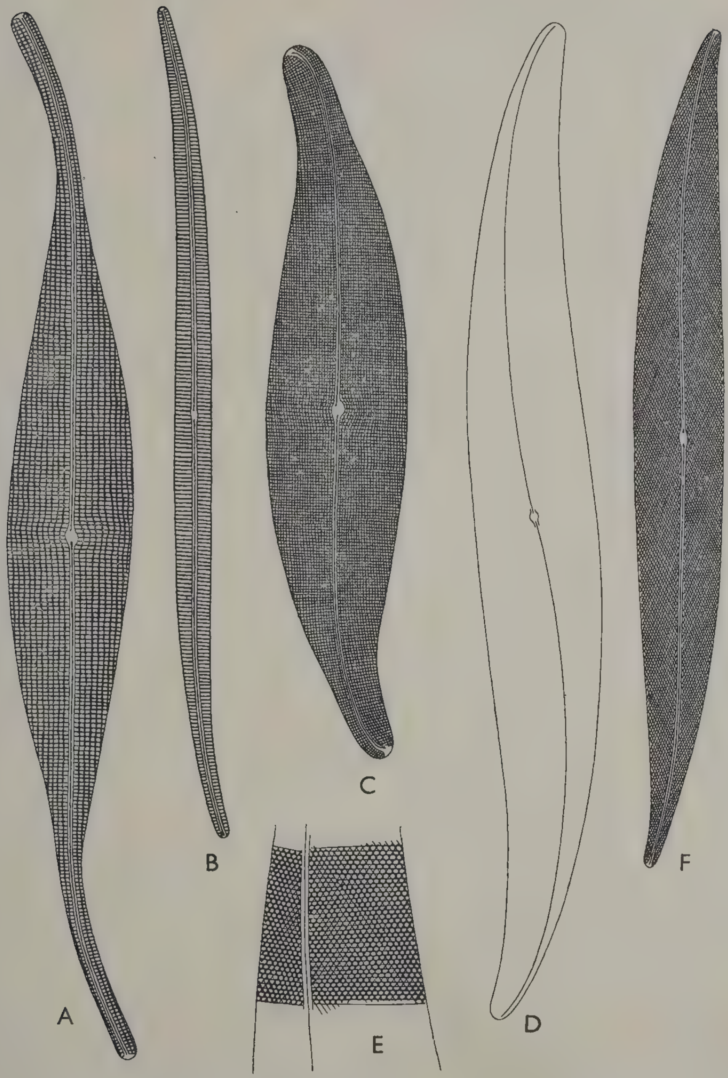

Fig. 2. A, *Gyrosigma fasciola* var. *sulcata* Grun. × 1200. B, *G. tenuissimum* (W. Smith) Cleve. × 1200. C, *G. distortum* (W. Smith) Cleve. × 1200. D, *Pleurosigma maroccanum* Cleve. × 600. E, part of same. × 1200. F, *P. subhyalinum* Hust. & Al, n.sp. × 1200. F.H. ad nat. del.

var. *sulcata* Grun. (Cleve, 1894. Van Heurck, 1880–5, pl. 21, fig. 7). More frequent than the typical form, from which it is distinguished by the stronger longitudinal striae (Fig. 2A).

*G. distortum* (W. Smith) Cleve (Hustedt, 1930*a*, p. 224, fig. 334). Not rare. The ends of the valves found are less protracted and more obtuse than described in the literature. (Fig. 2C).

*G. littorale* (W. Smith) (Cleve, 1894, p. 116). Rather rare. A very characteristic species, distinguished especially by the distant longitudinal lines.

*G. tenuissimum* (W. Smith) (Cleve, 1894, p. 117). Rather rare. Transapical striae 20 in 10 μ, longitudinal ones much denser, scarcely to be seen. (Fig. 2B).

### Genus **Pleurosigma** W. Smith

*Pleurosigma angulatum* (Quek.) W. Smith (Cleve, 1894, p. 40). Rare.

*P. aestuari* Bréb. (Cleve, 1894, p. 42). Frequent.

*P. Normani* Ralfs (Cleve, 1894, p. 40). Rather rare.

*P. naviculaceum* Bréb. (Cleve, 1894, p. 36). Rather frequent. The structure is coarser in the middle part of the valves, becoming denser towards the ends. In this respect it agrees with *P. Normani* and it seems that *P. Normani* comprises only the larger specimens of *P. naviculaceum*. In this paper we leave the two species separate until Hustedt's studies of the genus for the publication in the *Kieselalgen* are finished.

*P. subhyalinum* **sp.nov.** Valva sigmoidea, apicibus acutis, circiter 105 μ longa, 11 μ lata. Raphe sigmoidea centrali, area axiali nulla, area centrali parvissima. Structura delicatissima, striis obliquis 32–36 in 10 μ, sub angulo 45–50° decussatis, striis transapicalibus inconspicuis, 28–30 in 10 μ. (Fig. 2F).

Valves slender, hyaline, sigmoid with acute ends, length about 105 μ, breadth 11 μ. Raphe sigmoid, central, axial area absent, central area very small. Structure very delicate, only to be resolved in a medium with high refractive index, oblique striae 32–36 in 10 μ, crossing each other with an angle of 45–50°. Transapical striae inconspicuous, 28–30 in 10 μ.

The structure of the valve in this species is perhaps akin to *P. hyalinum* Grun. (Cleve & Grunow, 1880, p. 52), later cited by Cleve (1894, p. 42) in a note with *P. javanicum* Grun. However, neither Grunow nor Cleve has given any figure of this species and concerning the number of striae they state only that these are 'too delicate for measuring'.

It has been the experience, however, in dealing with the species belonging to *Pleurosigma* to take into consideration two important characters, namely: the exact shape of the valve with its raphe, and the number of striae. But since neither of these conditions has been satisfied in *P. hyalinum* Grun., we find ourselves unable to refer our specimen to this species and we prefer to keep it separate.

*P. obscurum* W. Smith (Cleve, 1894, p. 43). Rather rare.

*P. formosum* W. Smith (Cleve, 1894, p. 45). Not rare, but mostly in fragments.

*P.* (*Rhoicosigma*?) *maroccanum* Cleve (Cleve, 1894, p. 42). (*Rhoicosigma maroccanum* Cleve in Peragallo, 1893, p. 32, pl. 9, fig. 22). Very rare. Cleve considers this a doubtful species, requiring further examination. There exists only one figure of it made by Peragallo, which was copied by the same author (1897–1908, pl. 36, fig. 1). For these reasons and because of the fact that we found only a single valve in our samples which we are sure belongs to this species, we prefer to give a figure and a short description of our specimen.

Valve distinctly sigmoid with rather acute ends, length 250 $\mu$, breadth 30 $\mu$! Raphe more sigmoid than the valve (therefore strongly excentric towards the ends!). Oblique striae about 17 in 10 $\mu$, transapical striae about 19 in 10 $\mu$. Central area very small (Fig. 2 D, E).

The valve is slightly bent in the transapical axis as in species belonging to the genus *Rhoicosigma*. On the other hand, in this latter subgenus, unlike *Pleurosigma*, the two valves are different in shape. Since the second valve in *P. maroccanum* seems not to be known (at least not mentioned in the literature), it is doubtful whether the two valves belonging to the same frustule of *P. maroccanum* differ at all.

### Genus **Amphiprora** Ehr.

*Amphiprora paludosa* W. Smith (Hustedt, 1930*a*, p. 339, fig. 624). Rather frequent.

*A. pulchra* var. *pulchella* (Peragallo, 1897–1908, pl. 37, figs. 4, 5). Rare.

*A. sulcata* O'Meara (Peragallo, 1897–1908, pl. 38, figs. 1–3). Rather rare.

### Genus **Tropidoneis** Cleve

*Tropidoneis Vanheurcki* Grun. (Peragallo, 1897–1908, pl. 40, figs. 12, 13). Frequent.

*T. vitrea* W. Smith (Peragallo, 1897–1908, pl. 41, figs. 7, 8). Frequent. The last two species are generally distributed in mud-flats.

### Genus **Auricula** Castr.

*Auricula dubia* Peragallo (Peragallo, 1897–1908, pl. 42, figs. 8–11). Only a single specimen found.

### Genus **Amphora** Ehr.

#### Subgenus **Amphora** Cleve

*Amphora proteus* Greg. (Cleve, 1895, p. 103). Frequent, widely distributed in all marine coasts.

*A. marina* (W. Smith) Van Heurck (Cleve, 1895, p. 103). Rather frequent, this species is similar to the previous one, with which it may be united.

### Subgenus **Halamphora** Cleve

*Amphora coffaeiformis* Ag. (Hustedt, 1930*a*, p. 345, fig. 634). Very common. Also common on other mud-flats as well as on the rocky shore. The species is very variable. Many small species of *Amphora* have been described which probably belong to this species.

var. *acutiuscula* (Kütz.) (Hustedt, 1930*a*, p. 346). Rather frequent. Structure coarser than in the species. Both the species and its variety are of wide distribution both in marine coast lines and in salt lakes and ponds. They are able to stand a rather wide variation of pH.

*A. costata* W. Smith (Cleve, 1895, p. 122). Rare.

*A. turgida* Greg. (Cleve, 1895, p. 123). Rare.

### Subgenus **Oxyamphora** Cleve

*Amphora lineolata* Ehr. (Hustedt, 1930*a*, p. 346, fig. 636). Frequent.

*A. hyalina* Kütz. (Cleve, 1895, p. 127). Very rare, distinguished by its semicircular valve in girdle view, structure hyaline.

*A. arcus* Greg. (Cleve, 1895, p. 127). Not rare.

*A. ostrearia* Bréb. (Cleve, 1895, p. 129). Common. Similar to *A. arcus*, but distinguished by its narrow stauros.

*A. laevis* var. *laevissima* Greg. (Cleve, 1895, p. 130). Rare.

### Subgenus **Psammamphora** Cleve

*Amphora ocellata* Donk. (Cleve, 1895, p. 133). Rare.

### Subgenus **Cymbamphora** Cleve

*Amphora angusta* (Greg.) (Cleve, 1895, p. 135). Rather frequent.

## Genus **Gomphonema** Ag.

*Gomphonema exiguum* Kütz. (Cleve, 1894, p. 188). Rare.

## Genus **Rhopalodia** O. Müller

*Rhopalodia musculus* (Kütz.) O. Müll. (Hustedt, 1930*a*, p. 392, fig. 745). Not rare, but more common in brackish water.

## Genus **Cylindrotheca** Rabh.

*Cylindrotheca gracilis* (Bréb.) Grun. (Hustedt, 1930*a*, p. 393, fig. 746). Rather frequent, this species could easily be overlooked because of its hyaline structure. It belongs to the Nitzschiaceae and is characterized by its spirally twisted keels.

## Genus **Nitzschia** Hass.

### **Tryblionellae**

*Nitzschia punctata* (W. Smith) Grun. (Van Heurck, 1880–5, pl. 57, figs. 19, 20). Frequent.

var. *coarctata* Grun. (Hustedt in Schmidt, 1874–1944, pl. 330, fig. 16). Frequent.

*N. acuminata* (W. Smith) Grun. (Hustedt, 1930*a*, p. 401, fig. 764). Rather frequent.

*N. apiculata* (Greg.) Grun. (Hustedt, 1930*a*, p. 401, fig. 765). Frequent.

**Dubiae**

*Nitzschia commutata* Grun. (Hustedt, 1930*a*, p. 405, fig. 774). Rare.

*N. littorea* Grun. (Van Heurck, 1880–5, pl. 59, fig. 21). Rather rare, found only in the *Vaucheria* community. Characterized by the very distant median keel-puncta.

*N. dubiiformis* Hustedt (Hustedt, 1939, p. 658, figs. 111–113). Very common in the mud-flats. First described from the German coast, where it is also very frequent, especially on the sandy flats. It is characterized by its hyaline valves, dense striae and by its very variable number of keel-puncta which vary from 10 to 18 in 10 μ, the two median ones are more distant than the others.

**Panduriformes**

*Nitzschia panduriformis* Greg. (Hustedt in A.S. Atl. pl. 331, figs. 19–21). Rather rare. Much more frequent on warmer coasts.

*N. constricta* (Greg.) Grun. (Van Heurck, 1880–5, pl. 58, fig. 8). Rather common.

**Lanceolatae**

*Nitzschia aequorea* Hustedt (Hustedt, 1939, p. 663, fig. 120). Rather rare, characterized by its typical lanceolate valves, acute ends, small size and dense striae, which are about 35 in 10 μ.

**Sigmoideae**

*Nitzschia sigma* (Kütz.) W. Smith (Hustedt, 1930*a*, p. 420, fig. 813). Common.

**Spathulatae**

*Nitzschia angularis* W. Smith (Van Heurck, 1880–5, pl. 62, figs. 11–14). Not infrequent.

*N. distans* Greg. (Peragallo, 1897–1908, pl. 73, fig. 3). Common.

**Dissipatae**

*Nitzschia macilenta* Greg. (Peragallo, 1897–1908, pl. 72, figs. 1, 2). Rare.

*N. socialis* Greg. (Peragallo, 1897–1908, pl. 72, figs. 7, 8). Rather frequent.

**Pseudonitzschiae**

*Nitzschia pungens* Grun. (Cleve & Möller, 1882, Diat. No. 307, Cleve, 1897, p. 24, pl. 2, fig. 23). Rare. This species has hitherto been only known from Japan, and apart from the above two references there is no other mention of it in the literature. Cleve describes a variety *atlantica* from the Kattegat with somewhat denser striae (15 in 10 $\mu$), but our specimens agree more with the species than with this variety (length 100 $\mu$, breadth 4·5–5 $\mu$, striae about 10 in 10 $\mu$).

The species is akin to *Pseudonitzschia sicula* Castr., *P. migrans* Cleve and *P. seriata* Cleve figured in Peragallo (1897–1908, pl. 72, figs. 25–29) under the group Pseudonitzschia. The constriction of cell is not yet exactly known in this group, in which no keel-puncta are to be seen and that is perhaps the reason why some of the species included have been referred to *Synedra*.

Further studies are required in order to show the taxonomic position of this group and to elucidate the relation between the different species and until this is done we retain the original nomenclature of Grunow.

**Nitzschiellae**

*Nitzschia closterium* (Ehr.) W. Smith (Hustedt, 1930*a*, p. 424, fig. 822). Very common. Also widely known in the plankton. It was rather common in the plankton off Plymouth in March.

*N. longissima* (Bréb.) Ralfs (Schmidt, 1874–1944, pl. 335, figs. 1, 2). Not infrequent on the mud-flats.

### Genus **Surirella** Turp.

*Surirella ovalis* Bréb. (Hustedt, 1930*a*, p. 441, figs. 860, 861). Rare.

*S. gemma* Ehr. (Van Heurck, 1880–5, pl. 74, figs. 1–3). Frequent.

*S. fastuosa* Ehr. (Peragallo 1897–1908, pl. 58, figs. 5–7). Rather rare.

*S. caspia* Brun (Brun, 1891, p. 45, pl. 13, fig. 6). *S. cardaria* Brockmann (Brockmann, 1914, p. 70, fig. 11). Rare; only in the *Vaucheria* community.

This is an interesting species of which little is known. Apart from the figure given by Brun, his description of this species is quite insufficient. The only other mention, according to our knowledge, is a record by Meister (1932, p. 24) among a list of diatoms from the mouth of Belawan river in Sumatra. In the collection of Hustedt is to be found the original material of *Surirella caspia* Brun from the Caspian Sea, as well as that of *S. cardaria* Brockmann from the mouth of the Weser. These two species are identical, and we quote Brockmann's species as a synonym of *S. caspia* Brun and give the following description of the latter:

Cells with heteropolar apical axis, slightly twisted round this axis. Valves more or less broadly ovate to nearly orbicular, with obtusely rounded ends, 50–120 $\mu$ long, 36–60 $\mu$ broad. Ales broad, with distinct projection, primary alar canals broader than the windows, 10–20 in 100 $\mu$. Below the alar border-canal (see Appendices I and II), the primary alar canals are divided by short ribs into two to five secondary alar canals. Surface of the valve distinctly undulated. The crests of these undulations end on the ales in broad and flatly rounded arcs, while towards the median line the furrows are broader than the crests. Median area more or less developed, though not sharply defined. Transapical striae coarse, about 12 in 10 $\mu$ near the border of the valve. Short spines are scattered all over the surface of the valve, specially on the crests.

### Genus **Campylodiscus** Ehr.

*Campylodiscus Thureti* Bréb. (Peragallo, 1897–1908, pl. 57, figs. 8, 9). Very rare, only one specimen was found in the *Vaucheria* community. More frequent on warmer coasts.

## DISCUSSION

The species recorded in this paper are similar to those inhabiting mud-flats at Whitstable, Kent (Aleem, 1949). Many are also recorded by Hustedt (1939) from mud-flats on the German coast. Such marine mud-flats are, as a rule, rich in species belonging to the Raphidae, particularly those of the genera *Amphora*, *Gyrosigma*, *Navicula*, *Nitzschia*, *Pleurosigma* and *Tropidoneis*. These possess a well-developed raphe and are capable of moving freely within the substratum (Aleem, 1950*a*). They are to be found on the flats all the year round, though in varying degrees of abundance in the different seasons.

The mud-flats also comprise, in less significant quantities, other species which are recruited from three different sources, namely: (i) attached forms from the rocky shore, (ii) pelagic forms from the plankton, (iii) fresh-water forms from rivers and lakes. The last of these is much less significant than the others. Among those recruited from the rocky shore and found on the flats at the Salstone are species of *Cocconeis*, *Achnanthes*, *Licmophora*, *Grammatophora* and *Rhabdonema*. They are mostly colonial forms which grow attached by gelatinous stalks to rocks or as epiphytes on algae. Such forms were represented on the bare mud by only a few detached individuals, owing to lack of a proper substratum. A number of them, however, were much more frequent as epiphytes on seaweeds, especially in the *Vaucheria* community at M.L.W.S. The following diatoms are the principal species recognized from this community during the period of collection:

*Achnanthes longipes*
*Amphora coffaeiformis*
*A. hyalina*
*Cocconeis scutellum*
*Grammatophora marina*
*Licmophora gracilis* var. *anglica*
*L. flabellata*
*L. Juergensi*
*Opephora marina*
*Synedra Gailloni*
*S. tabulata*

Among those recruited from the plankton and to which reference has been made in this paper are the following species:

*Actinoptychus undulatus*
*Coscinodiscus centralis*
*C. excentricus*
*C. radiatus*
*Eucampia zoodiacus*
*Hyalodiscus scoticus*
*Nitzschia pungens*
*Roperia tessellata*
*Sceletonema costatum*
*Thalassionema nitzschioides*
*Thalassiosira decipiens*
*Thalassiothrix longissima*

They are mostly centric forms, rare on the mud-flats, and their presence here accidental. Most of them are more frequent in the plankton off Plymouth during March. No species of the genera *Chaetoceros* or *Rhizosolenia* were met with, neither as vegetative cells nor as resting spores, in our samples from the mud-flats, although these two genera were richly represented in the Plymouth plankton.

Apart from these, there are species which thrive equally well both in the plankton and in the littoral region. A conspicuous example of these is *Nitzschia closterium* which is found in appreciable quantities on all mud-flats, in littoral and supra-littoral pools as well as among the plankton. It is also known as a bottom form able to live in less well-oxygenated conditions (Mare, 1942). *Melosira moniliformis*, *M. sulcata* and *Biddulphia aurita* are also examples which are equally abundant both in the littoral region and in the plankton. It is more probable, however, that the origin of such species is in the littoral region and that later on they are recruited into the plankton, where they still retain the capacity to multiply.

## SUMMARY

A systematic study of the marine diatoms inhabiting the mud-flats at the Salstone, South Devon, is given. Altogether 132 species and 9 varieties, belonging to 45 genera are mentioned. Among these the following are described as new species: *Cocconeis guttata*, *Navicula aleemi* Hust., *N. britannica*, *Pleurosigma subhyalinum*.

Four other little-known diatoms, namely, *Achnanthes lilljeborgei*, *Nitzschia pungens*, *Pleurosigma maroccanum* and *Surirella caspia*, have also been found in the same locality and a detailed description of these is given. The Salstone diatoms are in essential respects similar to those found in other European north Atlantic mud-flats.

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## APPENDIX I

It has become necessary with the advance of our knowledge of diatoms due to modern microscopy to introduce some new terms describing certain configurations in the structure of the valve. Some such terms have already been proposed in the German literature by R. Lauterborn, O. Müller and Fr. Hustedt for which no equivalent translations have yet been given. We therefore propose the following translations of such German terms as we have used in this respect in our paper.

'Raphenschale' (*sensu* Hustedt, 1930*a*, p. 188) = raphe-valve.

'raphenlose Schale' (*sensu* Hustedt, 1930*a*, p. 188) = rapheless valve.
'Flügelrandkanal' (*sensu* Lauterborn, 1896, p. 15 = Querkanal) = alar border canal.
'Fenster' (*sensu* O. Müller, 1903, p. 24) = windows (for the intervening spaces between the alar canals of *Surirella*, also equivalent to the keel puncta in *Nitzschia*).
'Wellenberge' (*sensu* Lauterborn, 1896, pp. 14, 15) = crests.
'Wellentäler' (*sensu* Lauterborn, 1896, pp. 14, 15) = furrows.

The last two terms describe the undulations of the valve of *Surirella*. The word 'crest' had already been adopted by others, while 'Wellentäler' was formerly translated by 'hollows'. We prefer the term 'furrows' which seems to be more appropriate for the structure in question, and we suggest that the word 'depressions' might better be applied to the space between the median line and margin (in the valve of *Surirella*) in apical direction.

'Schleifenköpfe' (*sensu* O. Müller, 1903, p. 25) = arcs.
'Primärkanäle' = primary canals (see appendix II).
'Sekundärkanäle' = secondary canals (see appendix II).
'sekundäre Fenster' = secondary windows (see appendix II).

## Appendix II

### *Additional note on the construction of the ales in* Surirella

By Fr. Hustedt

Lauterborn (1896, pp. 14–16, pl. 1, figs. 8–12) made an intensive study of the structure of the ales in *Surirella calcarata* Pfitz. Most other species of this genus, specially the fresh-water forms, have ales identical with those of the latter species. Since many marine species of the genus deviate from it in structure, it is necessary to give here some additional remarks.

In many species the crests on the surface of the valve are very enlarged towards the basis of the ales, so that the alar canals become very broad too. In such cases narrow ribs or small windows project from the inner wall of the border canal into these enlarged alar canals in varying degrees, thus dividing the mouth of the alar canals into more or less numerous small openings. I have called the original alar canals 'primary canals', the smaller ones inside the latter 'secondary canals', and the spaces left between two adjacent canals 'secondary windows'.

# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### Floor of the English Channel

By W. B. R. King

*Geol. Mag.*, Vol. LXXXVII, 1950, pp. 383–4

Cores of the solid rock as well as the superficial cover have been obtained with a modified Stetson corer worked from the R.V. *Sabella* of the Marine Biological Association. Three areas have been sampled: (1) near the Eddystone, where New Red Sandstone has been proved over a wide area, while Chalk was found 18 miles south of the lighthouse; (2) mid-Channel, between Isle of Wight and Cherbourg, where Chalk was proved in the northern parts and Wealden sands and Jurassic clays in the central area, with Chalk again to the south; (3) an area crossing the Hurd Deep, W.N.W. of Guernsey to about mid-Channel, where the bed rock proved to be mostly Chalk. The research is continuing. W.B.R.K.

### Two new Pycnogonids from Bermuda

By Marie V. Lebour

*Proc. Zool. Soc. Lond.*, Vol. 118, 1949, pp. 929–32

Two new species of pycnogonid are described, *Anoplodactylus tenuirostris* and *Parapallene bermudensis*. The first a small species from the Reach, probably related to *A. petiolatus*, the second, one specimen only, from open water about 100 feet depth, near the bottom. M.V.L.

### Some new Decapod Crustacea from Bermuda

By Marie V. Lebour

*Proc. Zool. Soc. Lond.*, Vol. 118, 1949, pp. 1107–17

A new species of *Discias* and three species of *Periclimenes* are described.

The *Discias* was captured near the bottom, 100 ft. or more, in open water. Only three species are so far known and this new one is peculiarly interesting, the specialization of the first and second legs being unusually marked, but the mandible and maxilla showing a more primitive condition. The larvae of *Periclimenes iridescens* n.sp. were hatched from the egg and are interesting in being intermediate between *P. diversipes* and the typical *Periclimenes* (*Ancylocaris*) larvae described by Gurney.

It was found that the specific name of *P.* (*Ancylocaris*) *bermudensis* n.sp. was preoccupied and this was altered to *rhizophorae*. M.V.L.

## SOME EUPHAUSIDS FROM BERMUDA

By **Marie V. Lebour**

*Proc. Zool. Soc. Lond.*, Vol. 119, 1949, pp. 823–37

A collection of euphausids is described, following the work of Gurney (1947) and filling in certain gaps in this work. For the first time a nauplius of *Stylocheiron* is recognized, having hatched from the egg of *S. carinatum*. Certain variations in pleopod succession are noted in various species. M.V.L.

## NOTES ON SOME LARVAL DECAPODS (CRUSTACEA) FROM BERMUDA

By **Marie V. Lebour**

*Proc. Zool. Soc. Lond.*, Vol. 120, 1950, pp. 369–79

The larvae of *Panulirus argus* were hatched out and the first stage figured. Notes on later stages are given and descriptions of two larval scyllarids. Late stages of *Petrolisthes armatus* are described and two interesting zoeae of raninids. No species of adult *Ranina* has as yet been recorded from Bermuda. Some crab zoeae hatched from the egg are described—*Portunus spinimanus*, *Lobopilumnus agassizii* and *Grapsus grapsus*. M.V.L.

## SWIMMING OF DOLPHINS

By **G. A. Steven**

*Science Progress*, No. 151, 1950, pp. 524–5

Some years ago, while the author was serving in a ship on passage with another vessel in tow, a unique opportunity arose of obtaining exact observations of the time taken for dolphins to swim a known distance and so calculate their speed. It was found that some animals were capable of almost exactly 20 knots. The number of tail beats in animals swimming at 9 knots were also noted. The counts varied from 23 to 27 beats in 10 sec. Certain interesting characteristics of dolphin wakes are also described. G.A.S.

## DIFFERENTIATION OF THE SEA-URCHIN EGG FOLLOWING REDUCTION OF THE INTERIOR CYTOPLASM IN RELATION TO THE CORTEX

By Sven Horstadius, I. J. Lorch and J. F. Danielli

*Exp. Cell. Res.*, Vol. 1, 1950, pp. 188–93

The central cytoplasm of eggs of *Echinus esculentus* L. and *Psammechinus miliaris* (Gmelin) was reduced by suction before fertilization. The total cytoplasmic reduction amounted to about 50%.

In 20 eggs which started development no deviations in either animal or vegetal direction were observed. The resulting plutei were normal in every respect except size.

The results are contrary to Dalcq's concept of the differential localization of gradients at the centre and periphery of the sea-urchin egg. J.F.D.

## THE MECHANICS OF THE BLOOD VASCULAR SYSTEM OF *ASCIDIELLA ASPERSA*

By C. A. Haywood and H. P. Moon
University College, Leicester

*Journ. Exp. Biol.*, Vol. 27, 1950, pp. 14–28

The blood vascular system of *A. aspersa* is considered with particular reference to the well-known periodic reversal of the heart beat. It is emphasized that the problem involves two considerations: (1) why the heart stops beating periodically, and (2) why having stopped it should then reverse. The first consideration is taken in some detail and a mechanical model of the blood vascular system is considered mathematically. It is shown that a 'back pressure' similar to that postulated by La Hille arises, and that the heart should exhibit the periodic cessation of beating. A relation is deduced connecting the time between successive reversals with the velocity of the heart beat, and is shown to be capable of direct experimental verification. In this the ascidian is brought to various temperatures as a means of varying the velocity of the heart beat. Allowing for the variation of the viscosity of the blood with the temperature it is found that the relation is satisfied within certain limits, the significance of which is discussed.

Various criticisms of La Hille's 'back pressure' theory are shown to be invalid and examples are given of other closed contractile systems containing fluid which show reversal. H.P.M.

# BOOK REVIEW

## The Sea and its Mysteries

By John S. Colman

G. Bell and Sons, Ltd. 1950. Price 12*s.* 6*d.* net.

The most remarkable feature of this book is the facility with which Mr Colman puts into simple language so many recent physical and chemical discoveries about the sea. To make easy, and yet accurate, reading of details of wave motion, winds, ocean currents and the like and to sustain interest for page after page on these and other technical matters, usually considered difficult to expound, is no mean feat. The style is pleasant, the facts abundant and well assembled, the illustrations adequate and there are few blemishes. The result is a pleasurable book that should go far to stimulate interest in the science of the sea.

It is difficult to pick out any part for special commendation, each reader will have his or her own preference, but the chapter on coral reefs probably thrilled the reviewer more than any of the others. In a vivid piece of writing Mr Colman brings the wind-driven waves of the Pacific crashing through his pages and he adds all the colour and beauty of the Great Barrier Reef as well, or so it seems to one who has never been there. Mr Colman's own familiarity with so much of the sea the world over is very evident throughout; so often his writing is from first-hand experience and it is that above all else that makes the book live. It deserves success. D.P.W.

# GREGARIOUSNESS AND SOME OTHER ASPECTS OF THE SETTING BEHAVIOUR OF *SPIRORBIS*

By E. W. Knight-Jones

Marine Biological Station, Bangor

(Text-figs. 1, 2)

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## INTRODUCTION

Further study of the phenomenon of gregariousness during settlement, demonstrated in the oyster *Ostrea edulis* (Cole & Knight-Jones, 1949; Knight-Jones, 1951) and the barnacle *Elminius modestus* (Knight-Jones & Stephenson, 1950), seemed to require laboratory experiments, for which a viviparous animal with a brief, lecithotrophic, pelagic stage appeared to be needed.

In the Bangor area tube-worms of the genus *Spirorbis* are amongst the most abundant and easily obtained of such animals. They have proved to be excellent material for investigations on setting behaviour. This account deals mainly with *S. borealis*, the species which settles abundantly on *Fucus*, but some field observations and a single series of experiments on *Spirorbis pagenstecheri* are included.

Previous accounts of the behaviour of *Spirorbis* larvae are very incomplete and occasionally misleading. Shively (1897) observed attachment, but gave few details, Neu (1933) counted the numbers setting on plates of various colours, and Garbarini (1936*b*) made some observations which are referred to later (p. 214). Thorson (1946) gives further references.

This work was carried out in the Department of Zoology at the University College of North Wales, where Prof. F. W. Rogers Brambell, F.R.S., has

kindly given us rooms until our Station is built. I am very grateful to him and to his Staff for their hospitality and help. Dr H. A. Cole, of the Fisheries Experiment Station, Conway, encouraged me at an early stage with the information that his records of sessile organisms competing with oyster spat had given evidence of gregariousness in *Spirorbis*.

## Breeding Periodicity and Liberation of Larvae

*Fucus serratus* covered with *Spirorbis borealis* was collected frequently between late May and early October from near Bangor Pier at about low-water mark. Breeding was in progress throughout this period. Adults on pieces of *Fucus* were put into dishes containing about 200 ml. of sea water, into which the larvae were liberated.

Breeding periodicity in *S. borealis* was first demonstrated by Garbarini (1933), who found that liberations of larvae at Concarneau and Roscoff occurred only during a few days at each quarter of the moon. Later (1936*a*) he found that growth of oocytes to ripeness lasted about 14 days, that the incubation period was of similar duration, and that breeding was synchronized so that at each quarter a batch of larvae was liberated, a batch of eggs was spawned and a batch of oocytes began to grow. Liberations of larvae at Bangor showed similar periodicity. During July and August mass liberations occurred regularly during the few days before and after the moon's quarters. Very few larvae were obtained in the intervening periods. During June (when the weather was hot) breeding was less regular and less well synchronized. Many tubes were opened at various times and practically all contained embryos, which tends to confirm that a fresh spawning follows closely upon liberation.

Synchronization of breeding appeared to be less perfect than in Garbarini's material, for larvae were rarely unobtainable, but it proved to be a waste of time to attempt experiments except during the week in which each liberation peak occurred.

No larvae appeared for the first few minutes after adults were put into a dish. It seemed that a short period was needed to recover from disturbance, even if the adults were over-ripe for liberation. In freshly collected material only occasional individuals liberated their larvae, even during peak periods, but in material which had been in the laboratory for a few hours mass liberations of larvae could be obtained by (i) exposing to light dishes which had been kept for a few hours in the dark, (ii) changing the water of dishes, whether in the light or in the dark, (iii) immersing adults which had been kept out of water for a few hours or overnight. Such changes were various in their effects. The oxygen tension and pH were usually raised, but when the change was to fresh sea water from sea water which had contained brightly illuminated *Fucus*, both were lowered. Probably over-ripe adults will react by liberation to any improvement in their surroundings. Liberation appeared to be a voluntary act on the part of the adults because it was accompanied by marked protrusion of the body and by rocking movements, and because the larvae appeared helpless when they first emerged from the parent tube. They often remained motionless for about a quarter of a minute, entangled in the parent's tentacles. Then they gradually freed themselves and swam away towards the light. Usually twenty or thirty larvae, probably the whole brood, were liberated at the same time by each adult. Occasionally only two or three larvae made their appearance in a dish, suggesting that a few may be liberated before or after the majority of the brood.

## The Pelagic and Searching Phases

After liberation the larvae swam straight towards the light, each following in the path of the one in front. Swimming was relatively rapid, about 3 mm./sec. (the larvae being about 0·4 mm. long). It was largely or entirely effected by the large cilia of the prototroch. These showed metachronal waves which moved anticlockwise, seen from the apical end. The body rotated in the opposite direction.

The types of behaviour shown by larvae are summarized diagrammatically in Fig. 1. On reaching the lighted side of the dish the larvae swam backwards and forwards against the glass, usually near the surface of the water. They generally kept a straight course except when they hit an obstruction or found themselves going away from the light, when they turned and swam towards the light again, orientating directly towards it if free to do so. The length of this purely pelagic phase varied in different broods, but was usually between 15 min. and 2 hr.

After this period larvae frequently left the lighted side of the dish. Their swimming appeared rather random, with a photo-negative tendency. They generally swam straight, but if their course took them near a piece of *Fucus* they often turned and swam towards it as though able to perceive its dark surface. When kept for some hours in a clean glass vessel containing nothing suitable for attachment the majority collected near the bottom on the side remote from the light.

On making contact with a suitable surface a larva started to crawl on its ventral side at a speed of about 1 mm./sec., keeping a straight course unless it met an obstruction. On reaching the edge of a *Fucus* frond it generally crawled round on to the other side. Such a period of crawling rarely lasted more than a few minutes, and was sometimes very brief. The larva then swam off again. It often became positive to light for a further short period, before seeking another surface to crawl upon. Brief periods of swimming and crawling followed one another thus for 1 or 2 hr. During this time the larvae explored the dish thoroughly. They were often seen to encounter previously settled individuals, turn, crawl onwards, and eventually swim off again. They seemed to hurry about, with their entire output of energy given up to visiting as many different surfaces as possible.

The pelagic and searching phases were often much shorter in larvae liberated by parents which had been kept in crowded dishes or out of water for 1 or 2 days. Such larvae sometimes settled immediately they reached the glass side of the dish, if this bore a bacterial film. This behaviour appeared to be the result of long overdue liberation.

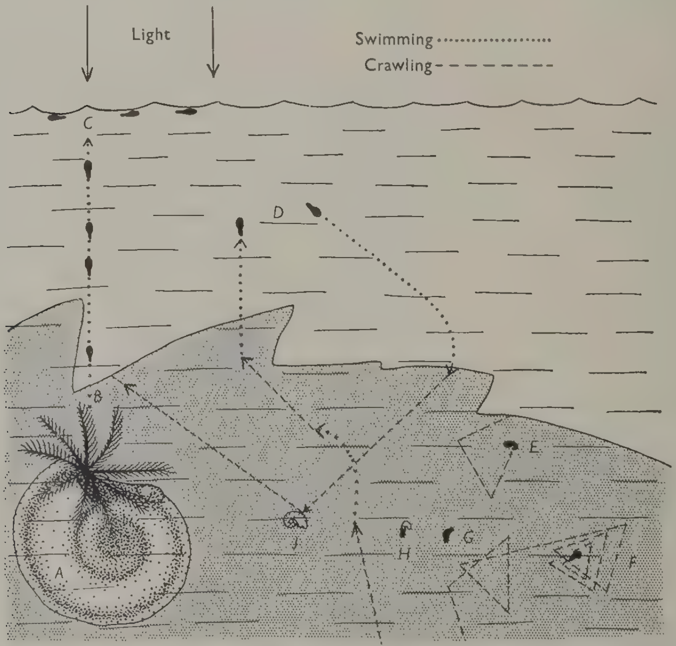

Fig. 1. Successive phases in behaviour of larvae of *Spirorbis borealis* illustrated diagrammatically. Stippled area represents frond of *Fucus serratus*. *A*, incubation within parent's tube; *B*, liberation and positive phototaxis; *C*, pelagic phase at surface; *D*, searching phase, with larvae swimming at random, or alternately negative and positive to light, interspersed with periods of crawling in straight lines; *E* and *F*, larvae about to settle and just settled, to show frequent changes of course during crawling; *G* and *H*, metamorphosis and formation of calcareous tube; *J*, individual 2 weeks after settlement.

## SETTLEMENT

A larva which was about to settle was recognizable by the fact that it frequently changed direction whilst crawling. During the straight crawling of the searching phase the narrow, tail-like abdomen remained projecting longitudinally, or occasionally twitched from side to side. When about to settle the posterior end of the abdomen was frequently pressed against the substratum, to which it appeared to adhere, and the abdomen was strongly flexed so that the trunk turned sideways, usually through an angle of about 120°. The larva crawled a short distance in the new direction before again using its abdomen to steer itself through another change of course.

A larva which had begun to change direction rarely swam off again, but often continued to crawl for many minutes and sometimes covered a few centimetres in its wanderings. Eventually it began to cross backwards and forwards many times over the area within 2 or 3 mm. radius of the spot upon which it was finally to settle. Crawling became gradually slower and turning more frequent until progress ceased and attachment took place. Very similar behaviour is shown by oyster larvae which are preparing to settle (Prytherch, 1934; Cole & Knight-Jones, 1939).

In the free-swimming larva of *Spirorbis borealis* there is a superficial white spot in the dorsal mid-line at the posterior end of the thorax, sufficiently large to be seen easily with a hand-lens. Under a low-power microscope this was seen to alter in shape when the body was flexed violently, as though it was a sac full of fluid. It may conveniently be termed the attachment gland from the part it plays during setting.

Immediately before setting movement in each direction was no more than about a millimetre before a flexure of the abdomen turned the body round. As crawling ceased the abdomen continued to wave from side to side and the whole body wriggled and alternately stretched and contracted, the muscles apparently taut and very active, but the movements slight. After a few seconds a cloud of milky liquid issued from the attachment gland, apparently through a narrow pore at its posterior end. The gland rapidly emptied and the fluid spread over the surface of the trunk and abdomen, losing its opacity during dispersion, and apparently forming the initial tube. The body continued to wriggle and rock about, as though to aid the dispersion of the fluid and to ensure adhesion to the substratum. Anteriorly, the folds of the collar, which had been pressed inconspicuously against the sides of the trunk in the free-swimming larva, became erected almost perpendicularly (see figures in Fewkes, 1885) and then bent backwards again. They appeared to be beginning to enclose and mould the anterior lip of the tube which was being formed. This is probably their function, for glands secreting the calcareous tube have been demonstrated under the collar of serpulids (Swan, 1950). Posteriorly, the body became shorter and broader, so that the previously abrupt demarcation between the broad trunk and narrow abdomen disappeared. The worm, with unceasing small movements, rolled first one way and then the other, and finally completely over ventral side upwards. The large, ventro-lateral eyes, which had been next to the substratum in the crawling larva, became very conspicuous as they faced upwards. The rudiment of the operculum, which was difficult to distinguish in the larva, now appeared on the left side of the head and grew with almost visible speed, whilst the head shrank so that the eyes, formerly widely separated, approached one another closely.

Fixation, shortening of the abdomen, and rolling ventral side upwards took place within 1 or 2 min. after crawling had ceased. Very striking growth of the operculum at the expense of the larval head took a further 5 or 10 min. The change was sufficiently rapid to be termed a cataclysmic metamorphosis. The trunk and abdomen were then enclosed in an almost transparent, straight tube, which, being only about 0·25 mm. long, could not accommodate the anterior end. This initial length of tube, derived wholly or in part from the secretion of the attachment gland, remained straight and semi-transparent, but a white, opaque, calcareous extension was added to it anteriorly. This gradually elongated and immediately started to bend to the occupant's left as the inner whorl of the future tube. About 5 hr. after settlement growth at the mouth of the tube had carried its axis through 90°. The occupant then had a large operculum and rudimentary tentacles, which it could withdraw completely into the tube.

## Need for Bacterial or Algal Filming of the Substratum

Surfaces immersed in sea water become covered with a film of micro-organisms after periods varying from a few hours to a few days (see ZoBell, 1946). There is evidence that larvae of a variety of sessile animals settle more readily on filmed surfaces than on clean surfaces (ZoBell & Allen, 1935; ZoBell, 1938, Scheer, 1945; Miller, Rapean & Whedon, 1948; Pyefinch & Downing, 1949; Cole & Knight-Jones, 1949).

Although previous accounts had described *S. borealis* as setting on glass, it was soon found that larvae in clean glass beakers metamorphosed only after a considerable delay. A series of experiments was carried out in which batches of larvae were divided between pairs of 50 ml. beakers. Each pair had contained sea water, with or without the addition of an algal culture (*Chlamydomonas* or *Synechococcus*) during the previous few days. One beaker of each was wiped clean with cotton-wool before use, the other was left with a visible film, which always included bacteria and was often coloured green with algal cells. The *Spirorbis* were examined after they had been in the beakers 24 hr. (Table I). In the aggregate 91 % had metamorphosed in the filmed beakers, only 15 % in the beakers which had been wiped. The results were consistent throughout with films of various origins.

A high proportion of larvae kept in clean beakers eventually became abnormal, showing some of the changes of metamorphosis, but a few retained the larval form for 2 or 3 days. The majority of these aged larvae lay motionless but some swam when disturbed. Five such larvae were placed, 48 hr. after liberation, in a flask which had contained a culture of the alga *Prasinocladus* and which bore a green film on the glass inside. After a further 24 hr. two of the five had metamorphosed and secreted tubes, showing that a greatly prolonged planktonic life may sometimes be followed by successful metamorphosis.

It was then found that the great majority of larvae would seek out and settle upon a filmed cover-slip in a clean beaker, and would not settle upon a clean cover-slip in a filmed beaker. Larvae encountering a filmed glass surface behaved differently from those encountering a clean one. On striking clean glass larvae either swam off again with no more than momentary hesitation, or swam over the surface with scarcely diminished speed. On striking a filmed surface they stuck to the film as soon as they touched it and then started crawling upon it at less than half the swimming speed. They appeared to have some difficulty in leaving a filmed surface. A larva about to swim away was often seen with its anterior end clear, its prototroch vigorously active, and its posterior end apparently attached to the surface by an invisible, gradually lengthening thread. Suddenly the larva would accelerate to normal swimming speed.

TABLE I. EARLIER METAMORPHOSIS OF *SPIRORBIS BOREALIS* IN FILMED BEAKERS THAN IN CLEAN BEAKERS

(In each experiment a batch of larvae was divided between a pair of 50 ml. beakers, one with the inside surface filmed, the other wiped clean. After 24 hr. the numbers metamorphosed and unmetamorphosed were counted. In all, 91 % had metamorphosed in the filmed beakers, 15 % in the clean ones.)

| Exp. no. | Origin of film | Nos. metamorphosed/ unmetamorphosed in | |
|---|---|---|---|
| | | Filmed beakers | Clean beakers |
| 1 | Beakers had contained sea water, to which a culture of *Chlamydomonas* had occasionally been added, for 14 days | 14/4 | 0/20 |
| 2 | | 16/2 | 4/15 |
| 3 | | 16/1 | 0/16 |
| 4 | | 21/5 | 1/21 |
| 5 | | 11/0 | 3/7 |
| 6 | | 30/0 | 6/24 |
| 7 | A culture of *Synechococcus* for 4 days | 12/1 | 0/17 |
| 8 | Sea water in dim light for 14 days | 21/0 | 9/10 |
| | Totals | 141/13 | 23/130 |

It seemed possible that clean glass might be too smooth for the larvae to crawl upon, so paired pieces of slate and granite, carefully matched, were selected as offering surfaces which were mechanically rough. One of each pair was immersed for 48 hr. in an algal culture (*Synechococcus* or *Prasinocladus*), the other was left dry. Then each pair was exposed to larvae in a 250 ml. dish. Many larvae encountered the freshly immersed stones, but none were seen to crawl upon them. Larvae that encountered the other stones, which were tinted green from the cultures in which they had been lying, immediately started to crawl. Eighty larvae settled on these stones, only two on the freshly immersed ones. (Table II).

It seems highly probable that *Spirorbis* settles on filmed surfaces rather than clean surfaces because it can crawl on them more easily, and that crawling is due to cilia sticking to bacterial films or algal surfaces. There is practically no interval between contact with a filmed surface and adhesion to it, so there is scarcely time for deliberate choice, but mechanical roughness is unlikely to be one of the factors involved.

TABLE II. LARVAE OF *SPIRORBIS BOREALIS* SOUGHT OUT FILMED SURFACES IN PREFERENCE TO FRESHLY IMMERSED ONES

(In each experiment larvae in a clean 250 ml. dish were presented with a pair of stones, one of which had been immersed in an algal culture for 48 hr., the other left dry for the same period immediately prior to the experiment.)

| Exp. no. | Stone | Culture | Nos. settled on stones which were: Filmed | Freshly immersed |
|---|---|---|---|---|
| 1 | Granite | *Synechococcus* | 36 | 0 |
| 2 | Granite | *Prasinocladus* | 18 | 0 |
| 3 | Granite | *Prasinocladus* | 4 | 2 |
| 4 | Slate | *Synechococcus* | 22 | 0 |
| Totals | | | 80 | 2 |

## EFFECT OF PREVIOUSLY SETTLED *SPIRORBIS* ON CHOICE OF SUBSTRATUM

*Fucus* was found to be suitable for settlement whether its surface had been wiped or not. When larvae were put into thoroughly wiped 250 ml. bowls with pieces of *F. serratus*, all the larvae settled on the *Fucus*, unless the bowls were placed in the dark, when many settled on the surface film. Similar behaviour during darkness has been recorded in *Bugula* (Grave, 1930; Lynch, 1949*a*). To avoid it most experiments were carried out in the light.

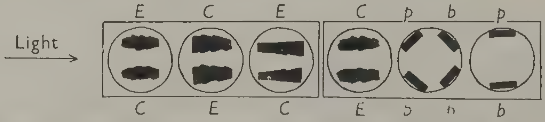

Fig. 2. In laboratory tests for gregariousness similar pieces of *Fucus*, some (*E*) bearing previously settled *Spirorbis borealis*, others (*C*) bare, were exposed side by side to larvae in 250 ml. dishes. These were contained in boxes which were white inside, both sides being equally illuminated. The diagram shows two boxes, each with three dishes. Results are given in Table III. Two dishes are shown with slate blocks, some bearing *S. borealis* (*b*), others *S. pagenstecheri* (*p*), which were used to test whether larvae could distinguish between the two species. Double pairs of blocks were used in Exps. 1–10 (see Table V), single pairs in Exps. 11–20.

As the larvae were photosensitive the dishes were placed in narrow boxes, white inside, the long axes of which were directed towards a window so that both sides appeared equally illuminated. For each experiment two similar pieces of *Fucus* were obtained from immediately above a dichotomy and placed on opposite sides of a dish, one bearing previously settled *Spirorbis*, the other a bare control. Experimental and control pieces were placed on alternate sides in adjacent dishes to guard against there being an undetected difference in illumination between the two sides (Table III). Freshly liberated larvae were then pipetted into the dishes in varying numbers.

TABLE III. SETTLEMENT OF *SPIRORBIS BOREALIS* ON TWO SEPARATE SIMILAR PIECES OF *FUCUS*, ONE WITH PREVIOUSLY SETTLED *SPIRORBIS*, THE OTHER BARE

(In every experiment, except those marked with asterisks (in which the larvae showed little discrimination or appeared to have been influenced by light), at least twice as many settled amongst the previously settled *Spirorbis* as on the bare *Fucus*.)

| Exp. no. | No. of previously settled *Spirorbis* | No. of larvae settling on | |
|---|---|---|---|
| | | Experimental *Fucus* | Bare control |
| 1 | 20 | 18 | 1 |
| 2 | 10 | 14 | 0 |
| 3 | 4 | 4 | 1 |
| 4 | 16 | 31 | 2 |
| 5 | 25 | 22 | 2 |
| 6 | 15 | 50 | 5 |
| 7 | 10 | 25 | 3 |
| 8 | 9 | 52 | 2 |
| 9 | 10 | 6 | 9* |
| 10 | 10 | 44 | 0 |
| 11 | 8 | 51 | 1 |
| 12 | 12 | 12 | 16* |
| 13 | 20 | 11 | 2 |
| 14 | 19 | 17 | 8 |
| 15 | 19 | 22 | 0 |
| 16 | 12 | 29 | 2 |
| 17 | 43 | 25 | 0 |
| 18 | 16 | 44 | 4 |
| 19 | 70 | 27 | 2 |
| 20 | 49 | 34 | 23* |
| 21 | 84 | 7 | 0 |
| 22 | 46 | 15 | 7 |
| 23 | 29 | 4 | 2 |
| 24 | 31 | 13 | 1 |
| 25 | 35 | 43 | 11 |
| 26 | 22 | 24 | 59* |
| 27 | 35 | 85 | 2 |
| 28 | 15 | 7 | 1 |
| 29 | 143 | 61 | 27 |
| 30 | 151 | 64 | 25 |
| 31 | 123 | 113 | 23 |
| 32 | 115 | 83 | 25 |
| 33 | 102 | 74 | 38* |
| 34 | 111 | 112 | 49 |
| 35 | 46 | 29 | 5 |
| 36 | 56 | 10 | 21* |
| 37 | 28 | 48 | 7 |
| 38 | 47 | 15 | 23* |
| | Totals | 1345 | 409 |

During this series of experiments the following conditions were varied, but the changes did not affect the results, which are given in Table III. At first, previously settled *Spirorbis* were removed from the controls. This often involved damage to the *Fucus* so similar damage was done to the surface of the other piece of each pair, either by removing tubes or by picking pieces away with the point of a needle. A few tests with bare pieces of *Fucus* indicated that damage discouraged settlement, so some experiments (nos. 8–11) were carried out in which the experimental pieces were more damaged than the controls. Later (nos. 17–24 and 29–34) the *Fucus* used was entirely undamaged, apart from the scissor cuts by which the pieces were obtained, and *Spirorbis* was allowed to settle on the experimental pieces shortly before the experiments, whilst the controls remained in neighbouring vessels which contained no larvae. In some experiments (nos. 12–16 and 29–34) the water in the dishes was kept circulating by air bubbles, in the remainder it was left unstirred.

In thirty-one out of the thirty-eight experiments the results were consistent, with a ratio of at least 2:1 in favour of the *Fucus* which bore previously settled *Spirorbis*. It is probable that some of the remaining seven experiments involved larvae which were in poor condition, for they were from adults which had been kept for 1 or 2 days in the laboratory. In the three experiments of these (nos. 26, 36 and 38) which showed a clear majority settling on the controls, it appeared that the dishes had not been equally illuminated, and that the larvae had been collecting towards their darker sides.

Altogether 1345 larvae settled on the *Fucus* which bore previously settled *Spirorbis*, 409 on the bare control pieces. In the earlier experiments (nos. 1–24) when the numbers of larvae in each dish varied between 5 and 57, over six times as many settled on the experimental pieces as on the controls. In the later ones, in most of which between 50 and 100 larvae were used, the ratio was only about 2·5:1. This recalls results obtained with *Ostrea edulis* (Cole & Knight-Jones, 1949), which showed that gregariousness tended to be masked when settlement was heavy, probably because a few less discriminating larvae settled early upon the control surfaces, thereby encouraging further settlement upon them.

## PROLONGATION OF THE SEARCHING PHASE IN ISOLATED INDIVIDUALS

The movements of larvae did not appear to be directed towards previously settled individuals, so it seemed probable that gregariousness might be accounted for by random swimming with settlement taking place more readily on *Fucus* which already bore *Spirorbis* than on bare *Fucus*. The possibility that metamorphosis might be delayed in isolated larvae was therefore investigated.

In each of three preliminary experiments 10 larvae were isolated in 50 ml. beakers, and 20 were put together into another similar beaker. To ensure, as far as possible, that the isolated and crowded larvae in each batch were comparable genetically, they were pipetted from a small liberation and put out alternately, one into isolation and two into the crowded beaker. All thirty may have come from the same parent. A piece of *Fucus* which bore five previously settled individuals was presented to the crowded larvae, pieces of bare *Fucus* to the isolated ones. The beakers were left under similar conditions of illumination and examined at intervals of about 20 min. When it was seen that most of the larvae in the crowded beaker had settled, the numbers which had metamorphosed and which were still moving were recorded, first in the crowded beaker and then in the other beakers. Because they were examined later the isolated larvae had a few minutes longer in which to metamorphose than the others. Nevertheless, it was found in each experiment that 85–95 %

Table IV. *Spirorbis borealis*. Percentages Metamorphosed in Experimental Batches of Larvae which were Crowded and or with *Fucus* Bearing Previously Settled Individuals and in Control Batches of Larvae which were Isolated with Bare *Fucus*

(Differences of less than 20 % are marked by asterisks. The other, more considerable, differences indicate consistently earlier metamorphosis in the experimental batches.)

| Exp. no. | Period (hr.) | No. of crowded larvae | Percentages metamorphosed | |
|---|---|---|---|---|
| | | | Experimental | Control |
| | Crowded with previously settled *Spirorbis* | | | Isolated |
| 1 | 3 | 20 | 90 | 60 |
| 2 | 1 | 20 | 95 | 70 |
| 3 | 1 | 20 | 85 | 40 |
| | | Mean | 90 | 57 |
| | Crowded with initially bare *Fucus* | | | Isolated |
| 1 | 2½ | 25 | 60 | 50* |
| 2 | 2 | 20 | 90 | 50 |
| 3 | 2 | 50 | 100 | 33 |
| 4 | 1½ | 100 | 95 | 75 |
| 5 | 1½ | 100 | 85 | 80* |
| 6 | 1½ | 45 | 98 | 90* |
| 7 | 1½ | 50 | 30 | 30* |
| 8 | 2 | 50 | 90 | 44 |
| 9 | 2 | 48 | 87 | 60 |
| 10 | 6 | 49 | 58 | 20 |
| | | Mean | 79 | 53 |
| | Single larvae with previously settled *Spirorbis* | | | Isolated |
| 1 | 2 | — | 44 | 10 |
| 2 | 1 | — | 78 | 70* |
| 3 | 1 | — | 89 | 20 |
| 4 | 1 | — | 90 | 60 |
| 5 | 1 | — | 100 | 70 |
| 6 | 1 | — | 50 | 60* |
| 7 | 3 | — | 100 | 60 |
| 8 | 3 | — | 70 | 30 |
| 9 | 3 | — | 80 | 56 |
| 10 | 1½ | — | 56 | 50* |
| | | Mean | 76 | 49 |

of the crowded larvae had metamorphosed, but only 40–70 % of the isolated ones (Table IV).

Using similar methods, a series of ten experiments was then carried out, in which the crowded larvae, between 20 and 100 in number, were presented with bare *Fucus*. In the aggregate 79 % of the crowded larvae metamorphosed, but only 51 out of the 96 isolated ones (the 4 remaining isolated larvae could not be found, having probably adhered to the inside of the pipette). Consistently in six out of the ten experiments 20–67 % more of the crowded larvae metamorphosed than of the others. In the remaining four experiments the differences were 10 % or less. This does not prove that the presence of unmetamorphosed larvae promotes settlement. The earlier settlement in the crowded beakers may possibly have been due to a few less discriminating larvae attaching themselves and metamorphosing, thus encouraging further settlement.

In each of another series of ten experiments twenty isolated larvae were divided into two batches, one of which was presented with pieces of *Fucus* bearing from 5 to 10 previously settled *Spirorbis*, the other with similar bare pieces. A total of 73 out of 96 larvae in the former batch metamorphosed, 48 out of 99 in the latter (the remaining larvae were lost). In seven out of the ten experiments 25–70 % more larvae metamorphosed in the former than in the latter. In the remaining three experiments the differences were 10 % or less.

The length of the period of larval life appeared to be rather similar in larvae from the same parent, but it varied widely in different batches. As Table IV shows, 100 % of one batch metamorphosed within an hour, but only 60 % of another in 6 hr. The results show that the searching phase was prolonged by isolation, but do not show by how much it was prolonged. As a mere conjecture, the prolongation often appeared to be about an hour. This is probably sufficient to account for the gregariousness shown in the laboratory experiments.

## Ability of Larvae to Distinguish their own Species from an Allied Species

*S. pagenstecheri* is abundant on stones and shells in the lower half of the tidal zone on most shores near Bangor. Its tube coils so that the mouth faces anticlockwise from an observer's viewpoint, whereas that of *S. borealis* is clockwise. Its larvae are colourless (apart from their red eyes) and very small, whereas those of *S. borealis* are much larger and reddish brown in colour.

*S. borealis* appeared to be rather more common on stones than *S. pagenstecheri* was on *Fucus*, so smooth slate was chosen as providing an experimental surface suitable for both species. Eight similar blocks measuring 24 × 24 × 4 mm. were prepared. These were immersed in sea water for a day, to allow a bacterial film to develop, and were then divided into two batches, with each block in a separate, freshly wiped beaker. Larvae of *Spirorbis borealis* were added to one batch, and larvae of *S. pagenstecheri* to the other. These soon settled on the blocks. The blocks were then exposed in pairs (Fig. 2), one of each pair bearing *S. borealis*, the other *S. pagenstecheri*, in 250 ml. dishes to which larvae of both species were added. After 24 hr. the numbers of both species which had settled on each block were recorded. The few *S. borealis* which had settled on the *S. pagenstecheri* blocks were then removed, whilst the *S. pagenstecheri* were removed from the other blocks. This was done with the point of a needle to avoid disturbing the bacterial films, which were probably similar on all the blocks since they had all been exposed under similar conditions for the same period. The experiments were then repeated.

TABLE V. *SPIRORBIS* LARVAE SETTLED AMONGST THEIR OWN SPECIES IN PREFERENCE TO AN ALLIED SPECIES

(In a series of experiments larvae of *S. borealis* and *S. pagenstecheri* were put together in a 250 ml. dish containing paired blocks of smooth slate, one of each pair bearing previously settled *S. borealis*, the other *S. pagenstecheri*. Inconsistent results are marked by asterisks.)

| | | | Nos. of larvae of | | | |
|---|---|---|---|---|---|---|
| | Nos. of previously settled | | *S. borealis* setting on blocks bearing | | *S. pagenstecheri* setting on blocks bearing | |
| Exp. no. | *S. borealis* | *S. pagenstecheri* | *S. borealis* | *S. pagenstecheri* | *S. pagenstecheri* | *S. borealis* |
| 1 | 18 | 58 | 20 | 6 | 26 | 10 |
| 2 | 34 | 65 | 6 | 3 | 29 | 14 |
| 3 | 40 | 90 | 21 | 3 | 43 | 5 |
| 4 | 58 | 132 | 30 | 10 | 16 | 7 |
| 5 | 92 | 70 | 12 | 7 | 7 | 5* |
| 6 | 4 | 24 | 38 | 14 | 24 | 29* |
| 7 | 32 | 35 | 56 | 6 | 40 | 13 |
| 8 | 83 | 71 | 15 | 4 | 3 | 14* |
| 9 | 93 | 72 | 18 | 33* | — | — |
| 10 | 30 | 49 | 1 | 0 | 16 | 0 |
| | | | Blocks changed round | | | |
| 11 | 4 | 7 | 9 | 0 | 7 | 1 |
| 12 | 13 | 14 | 12 | 0 | 7 | 1 |
| 13 | 25 | 21 | 17 | 1 | — | — |
| 14 | 5 | 12 | 8 | 1 | 7 | 1 |
| 15 | 13 | 19 | 5 | 2 | 12 | 1 |
| 16 | 12 | 4 | 7 | 0 | 9 | 1 |
| 17 | 19 | 13 | 9 | 0 | 17 | 3 |
| 18 | 5 | 1 | 6 | 0 | 1 | 0 |
| 19 | 11 | 2 | 6 | 3 | 10 | 3 |
| 20 | 14 | 12 | 11 | 1 | 8 | 0 |
| | | Totals | 307 | 94 | 282 | 108 |

After ten experiments the results seemed conclusive (Table V). In the aggregate, and in seven or eight out of ten separate experiments, more than twice as many larvae of each species settled on the blocks which bore their own species than on the other blocks. To guard against the possibility of there being some intrinsic difference between the blocks of each pair, the blocks were all wiped clean and changed round, so that those which had previously borne *S. borealis* bore *S. pagenstecheri* and vice versa. Another similar series of ten experiments was then carried out, using small numbers of larvae and taking care to obtain these only from freshly collected adults. The results which followed were still more conclusive. About 90 % of the larvae of each species sought out their own species in preference to the other.

It is scarcely conceivable that the larvae could have distinguished mechanically between their own species and the allied one. The tubes of the previously settled individuals grew quickly, so that the size ranges of the two species overlapped one another considerably. Those searching larvae which were seen to encounter tubes never paused to explore their shape or size, but always moved away immediately. It seems highly probable that some chemical sense played the main part in recognition of their own species.

## Further Aspects of the Behaviour during Settlement

Garbarini (1936*b*) carried out experiments on larvae from *S. borealis*, which he kept in an aquarium on a clump of *Fucus*. With circulating sea water he was able to keep them thus in good condition for more than 2 months. During the initial photopositive phase larvae attached themselves to every object which they could not go round, whatever its nature. Later they appeared to be attracted or repelled by neighbouring objects. Then, if a larva passed near *Fucus*, it went straight to the surface, crawled upon it and attached itself. Few larvae settled on *Laminaria* and still fewer on *Himanthalia*, *Ascophyllum*, *Rhodymenia* and stones and other inanimate objects. None attached to ascidians. *Botryllus* seemed repellant. He visualized the contrasting behaviour towards *Fucus* and *Botryllus* as due to substances secreted into the water by these organisms.

Similarly rapid settlement, without a searching phase, was observed at Bangor in larvae liberated by adults which had been kept in the laboratory for more than 1 or 2 days (p. 204). The apparent attraction towards *Fucus* may be a response of photonegative larvae towards the dark fronds (p. 203). A few experiments tended to confirm that *Fucus* is much more favourable for settlement than *Ascophyllum*. It has already been shown that freshly immersed inanimate surfaces are very unfavourable (p. 207).

*Fucus* is not overwhelmingly favourable for settlement. When larvae were put into a dish, the glass of which bore a bacterial film and some previously settled *Spirorbis* on its lighted side, they all settled on the glass amongst the *Spirorbis* though there was *Fucus* in the dish. Settlement on glass cover-slips bearing a bacterial film and 10 to 50 *Spirorbis*, which had settled a short time previously, was compared with settlement on a bare piece of *Fucus* of similar size. In a single experiment in the light 25 larvae settled on the *Fucus*, 5 on the cover-slip. It seemed likely that the searching larvae found the dark surface of the *Fucus* visually during their repeated reconnaissances, so four other experiments were carried out in the dark. In these 76 larvae settled on the cover-slip, none on the *Fucus*. Light and photosynthesis are complicating factors, but in the dark gregariousness was clearly stronger than a possible predilection for *Fucus*.

Fewkes (1885) noted that *Spirorbis* larvae in aquaria sometimes settled, metamorphosed and floated on the surface film 'until the increasing specific gravity of their bodies sinks them to their future homes', but it is very unlikely that re-attachment to another surface can occur after metamorphosis. At Bangor settlement on the surface film took place particularly readily in the dark and when there was a bacterial scum there.

TABLE VI. PROVIDED THE SURFACE WAS NOT CROWDED ($<10/\text{cm.}^2$) MORE LARVAE OF *SPIRORBIS BOREALIS* SETTLED ON *FUCUS* WHICH BORE MANY *SPIRORBIS* THAN ON SIMILAR PIECES WHICH BORE FEWER

(In each experiment larvae were presented with two similar pieces of *Fucus* of surface area 4–8 cm.$^2$, one bearing many more recently settled *Spirorbis* than the other.)

| | *Fucus* with many *Spirorbis* | | *Fucus* with few *Spirorbis* | |
|---|---|---|---|---|
| Exp. no. | (Nos. previously settled) | Larvae setting | (Nos. previously settled) | Larvae setting |
| 1 | (80) | 49 | (20) | 29 |
| 2 | (83) | 11 | (18) | 2 |
| 3 | (54) | 15 | (21) | 1 |
| 4 | (120) | 16 | (18) | 0 |
| 5 | (32) | 13 | (7) | 3 |
| 6 | (26) | 14 | (5) | 12 |
| 7 | (120) | 8 | (10) | 0 |
| 8 | (38) | 14 | (5) | 1 |
| Totals | | 140 | | 48 |

Settlement took place very frequently in concavities, such as the slight grooves alongside the midrib of *Fucus* or the angle at the periphery of a beaker's base. This was probably a response to contact stimuli. It could not be sheltering from currents or light when it occurred in still water and with a transparent substratum.

In eight experiments (Table VI) larvae attached in far greater numbers to *Fucus* which bore many recently settled *Spirorbis* (5–10/cm.$^2$) than to pieces which bore fewer (1–2/cm.$^2$), but the crawling larvae left areas which were crowded with 10–20 recently settled *Spirorbis* per cm.$^2$ and spaced themselves out very evenly on adjoining less crowded areas. In a further five experiments (Table VII), pieces bearing 1–4/cm.$^2$ proved to be more favourable for settlement than similar pieces crowded with 20–50/cm.$^2$. Apparently the gregarious tendency operates until it has led to a crowding of about 10/cm.$^2$, but larvae arriving thereafter try to find less crowded areas nearby.

This spacing out tendency is not due to physical lack of space because larvae proved to be capable of settling at over 40/cm.$^2$ when they were given no other choice. It must involve discrimination, which is probably exercised during crawling. The behaviour immediately prior to settlement is well suited to ensuring, as far as possible, that there is a clear area of 1 or 2 mm. radius round the place of attachment (p. 205, and Fig. 1).

A spacing-out tendency on very crowded surfaces has also been recorded in the barnacle *Elminius modestus* (Knight-Jones & Stephenson, 1950).

TABLE VII. MORE LARVAE SETTLED ON *FUCUS* WHICH BORE FEW *SPIRORBIS* THAN ON SIMILAR SMALL PIECES WHICH WERE VERY CROWDED ($>20/\text{cm.}^2$)

(In each experiment larvae were presented with two similar pieces of *Fucus* of surface area 1–2 cm.$^2$, one with few or no recently settled *Spirorbis*, the other crowded to an artificially high degree (the previously settling larvae having been given no other surface for attachment).)

| | *Fucus* with crowded *Spirorbis* | | *Fucus* with few *Spirorbis* | |
|---|---|---|---|---|
| Exp. no. | (Nos. previously settled) | Larvae setting | (Nos. previously settled) | Larvae setting |
| 1 | (53) | 10 | (4) | 37 |
| 2 | (62) | 9 | (2) | 16 |
| 3 | (59) | 11 | (3) | 11 |
| 4 | (50) | 14 | (0) | 20 |
| 5 | (63) | 11 | (5) | 30 |
| | Totals | 55 | | 114 |

## SOME FIELD OBSERVATIONS

Sample patches of *Fucus serratus* at different levels on the shore were examined during one of the periods in which *Spirorbis borealis* was liberating larvae. Recently settled individuals were numerous about low-water mark, particularly on the new growth bordering on old stems which were thickly covered with old *Spirorbis*. Very few were found on the abundant *Fucus* at about half-tide, which bore no older stages of *Spirorbis*, though a few laboratory experiments had indicated that *Fucus* collected from above half-tide was as favourable for settlement as some from low-water mark. One may speculate that liberations occurred during the ebb tide or at low water, so that larvae, settling within a few hours, got little opportunity of reaching the higher levels of the shore, but so far there is no evidence for such behaviour. It is probable that the heavy settlement at low-water mark, where adults were numerous, was largely due to the gregarious tendency, and that this usually prevents large numbers of larvae from settling at an unfavourably high level on the beach.

Very few *Spirorbis* were found on *Ascophyllum*, even in areas where this was intermingled with *Fucus* bearing abundant *Spirorbis* (see p. 214).

*S. pagenstecheri* was comparatively rare on *Fucus*, but when one individual was noticed on a frond a search generally revealed several others nearby. It was common on stones and shells in damp places in the lower half of the tidal zone. It is probably short-lived, for in many places the stones bore only tubes which were empty or occupied by *Polydora*. When the collection of adults for laboratory experiments was begun, much time was wasted in the difficult task of examining the tubes to see whether or not they contained live *Spirorbis*. Then it was noticed that amongst live tubes there were usually many very small but conspicuously white tubes of recently settled individuals, whilst no such concentrations of young individuals were to be found round dead tubes. This might suggest that the larvae had settled immediately after liberation, but laboratory observations showed that larvae from freshly collected adults were positively phototactic for at least a quarter of an hour after liberation, and usually for longer than this. Probably they are so in the field, which would lead to their being widely dispersed.

Shells of *Nucella lapillus* were often covered with *Spirorbis*, either with the dextral tubes of *S. pagenstecheri* or the sinistral tubes of *S. granulatus* or *S. borealis*. Whilst some *Nucella* bore tubes which were all dextral, others from the same area bore only sinistral tubes. Mixtures of two species on such a small area as a *Nucella* shell appeared to be comparatively uncommon. *Spirorbis* on rocks and stones occurred in clumps, often of a single species. Isolated individuals were comparatively rare.

These observations left a strong impression that the specifically gregarious tendency demonstrated in the laboratory was of great importance in the field.

## Gregariousness as Probably a General Feature of the Settlement Behaviour of Marine Larvae

Thorson (1950) found that about 70–80 % of bottom-living invertebrates have planktonic larvae, and reviewed the evidence that many of these larvae are able to postpone metamorphosis for days or even weeks, and to search actively for a suitable substratum. 'In a water area with a bottom current of only half a knot the larvae forced towards the bottom by their photonegativity and testing the substratum at intervals may be carried over a distance of 24 km. in 24 hr., i.e. 170 km. per week, and their chance of finding a suitable substratum for settling and metamorphosis seems to be great.' It is usually possible to relate the patchiness of the benthos to differences in the substratum, but sometimes it is difficult. *Pecten maximus*, for example, lives on a sandy bottom which may extend for vast areas, yet Priol (1930) described this species as essentially gregarious. During dredging near Bangor, in the wide sandy area of Red Wharf Bay, it was found commonly in some places but not at all in hauls from neighbouring, apparently similar, ground.

The distribution of marine animals is probably greatly influenced by the settlement behaviour of their planktonic larvae. In general, little is known about this behaviour. No evidence for gregariousness during settlement had been revealed when Allee (1931), having described crowded populations of certain littoral species, which appeared to be far below the level of organization at which a 'social appetite' was likely to occur, concluded that aggregations of primitive animals form frequently as the result of forced movements. This must be true. Berrill (1950) may well have been justified in describing the aggregations, which are usually typical of the ascidian *Styelopsis grossularia*, as due to the viviparous development and insensitivity of the tadpoles to light, factors tending to 'keep the children at home', though he gave the free-swimming period as of many hours.

In laboratory experiments on ascidian larvae (Grave, 1935, 1941, 1944; Grave & Nicoll, 1940) metamorphosis was hastened by crowding or by aqueous extracts of the adults or larvae.[1] This is suggestive. The distribution of ascidians often suggests specific gregariousness. In 1948 *Ascidiella aspersa* was abundant and *Ascidia conchilega* was comparatively sparse on certain oyster grounds worked from the Fisheries Laboratory at Burnham-on-Crouch, Essex. *Ascidia conchilega* occurred in clumps, with few isolated individuals, as though the larvae were gregarious and could distinguish their own species from the other.

So far tests for gregariousness have been carried out only on *Ostrea edulis*, *Elminius modestus* and the two species of *Spirorbis* dealt with here. These animals were not chosen for research because they were obviously more gregarious than other marine invertebrates, but because of their economic importance or convenience. The fact that the tests gave positive results in each species, representing three main phyla, suggests that gregariousness will prove to be a rather general feature of settlement behaviour. Though it has been demonstrated only in sessile species, in which it is likely to be particularly important, it will probably occur in others also, since most marine invertebrates have limited powers of locomotion as adults.

Andrews (1949), having observed that Folliculinidae constantly occurred in clumps, suggested that the behaviour could hardly serve for protection or feeding, but that breeding might be aided by clumping, if a process of conjugation occurred in the imperfectly known life cycle of the group. Breeding is likely to be the main advantage to be derived from gregariousness, but it is not the only one. Another is that larvae will probably find, in places where the species is already established, suitable conditions for their own survival.

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[1] Glaser & Anslow (1949) have suggested that this may have been due to copper, which they found to be present in ascidians and which has been shown to accelerate their metamorphosis. The grounds for this idea are weakened by the facts that (i) Grave (1935) found that tissue extracts which rapidly and consistently induced metamorphosis in larvae of the same species had at most only a slight effect on another species, and (ii) a variety of unfavourable conditions and dilute solutions of other poisons besides copper have been shown to accelerate metamorphosis, not only in ascidians (Zinkin, 1938), but in *Bugula* (Lynch, 1949*b*) and *Tubularia* (Pyefinch & Downing, 1949). The same criticism may now be made of Prytherch's conclusion that copper is necessary for metamorphosis in larvae of the American oyster. Prytherch (1934) put forward, in support of this, a controversial idea regarding the function of the pigment spots in the larval mantle (Cole, 1938) and an interpretation of some results, showing peak settlement at low water, which has also been questioned (Korringa, 1940). It should not yet be accepted that copper has a peculiar or necessary effect on metamorphosis in either oysters or ascidians.

This will be particularly important in species with closely restricted habitats. Often the factors which make places unsuitable for a species are complex or do not operate all the time. The presence of adults is a simple test of suitability. Without gregariousness many larvae of *S. borealis* would probably settle, during high water, on the *Fucus* in the upper half of the tidal zone, where they would be doomed to desiccation during subsequent ebbs (see p. 216).

Gregariousness in oysters proved to be most marked when settlement was light and to be masked when settlement was very heavy, probably because a few less discriminating larvae soon settled on bare surfaces, stimulating others to follow (Cole & Knight-Jones, 1949; see also p. 210). This phenomenon seems bound to accompany gregariousness in general and to have the following results, beneficial to the species. In poor breeding years settlement of larvae will be concentrated round the parent stocks, replenishing these as far as possible. This happened during the poor oyster spatfall of 1947 in the River Crouch, Essex (Knight-Jones, 1951). In normal breeding years old stocks will be built up and the range of the species may be extended to new areas, where pioneer larvae will be followed by others. In exceptionally good breeding years larvae will settle abundantly in every area to which they drift in sufficient numbers. Great increases in the range of the species will occur and many larvae will settle in unusual and often unsuitable places. Oyster larvae are said to have settled abundantly (and most unusually) on reeds in flooded ditches during the exceptionally good spatfall of 1935 in the River Crouch, Essex. Settlement in such places is mass suicide, but population pressure on the old beds is thereby reduced. This pressure may become too great in exceptionally good breeding years. At Conway, in 1940, practically all *Mytilus edulis* of marketable size were smothered and killed by a continuous covering of young mussels (Ministry of Agriculture and Fisheries, 1946, p. 57). In *Elminius* and *Spirorbis* the spacing-out tendency on crowded surfaces (p. 216) and the normally short span of life guards against such a disaster.

## SUMMARY

*Spirorbis borealis* and *S. pagenstecheri* were chosen for laboratory experiments on settlement behaviour because they are viviparous, with larvae which soon settle.

*S. borealis* liberated larvae mainly at about the moon's quarters.

After liberation larvae were positively phototactic for a period (15 min. to 2 hr.), then swam more at random. For a further period of 1 or 2 hr. they visited a large number of different surfaces, crawling upon them and then swimming off again.

When about to settle the crawling larvae changed direction with gradually increasing frequency by flexing the abdomen. Eventually they attached themselves, with wriggling movements, by the milky secretion of a gland on the

dorsal surface, which formed the initial, semi-transparent tube. Within 1 or 2 min. they rolled over on to the dorsal side and embarked upon a cataclysmic metamorphosis.

Larvae settled on surfaces of glass or stone only if the surfaces bore bacterial or algal films. In clean vessels larvae did not metamorphose, except abnormally or after a considerable delay, unless a filmed surface or a piece of *Fucus* was provided for attachment. Searching larvae did not stick to wiped or freshly immersed surfaces and appeared to be unable to crawl upon them, but immediately they touched filmed surfaces they stuck to them and started to crawl.

Many more larvae settled on pieces of *Fucus* which bore previously settled *Spirorbis* than on bare controls.

Settlement occurred earlier in larvae which were crowded, or accompanied by previously settled individuals, than in isolated larvae.

Paired slate blocks, one bearing previously settled *S. borealis*, the other *S. pagenstecheri*, were exposed to larvae of these two species. The great majority of the larvae settled on the blocks which bore their own species rather than on those which bore the other.

*Fucus* was very favourable for settlement of *S. borealis*, but in the dark bare *Fucus* proved less favourable than filmed glass surfaces which bore previously settled *Spirorbis*. Larvae often settled in concavities, probably in response to contact stimuli. Gregariousness soon led to a crowding of from about 10 to 20 recently settled individuals per cm.$^2$, but larvae arriving thereafter sought less crowded areas nearby, on which they spaced themselves out.

In the field settlement of *S. borealis* occurred mainly about low-water mark, on *Fucus* which already bore *Spirorbis*. Stones which bore live adult *S. pagenstecheri* could easily be distinguished from others which bore dead tubes, because many small, white tubes of recently settled individuals occurred amongst the adults.

Gregariousness during settlement has been demonstrated in each of the only four species so far investigated (*Ostrea edulis*, *Elminius modestus* and two species of *Spirorbis*), representing three main phyla. It is probably a general feature of the settlement behaviour of planktonic larvae, helping them to find suitable habitats, to maintain old breeding stocks and to form new ones.

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# ON THE BIOLOGY OF *MYTILICOLA INTESTINALIS* (STEUER)

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(Text-figs 1–3)

## INTRODUCTION

The copepod parasite *Mytilicola intestinalis* was first described by Steuer (1902) from the gut of *Mytilus galloprovincialis* (Lam.) in the Gulf of Trieste. Monod & Dollfus in 1932 recorded the same species from *M. edulis* from Marseilles. In 1939 the parasite was first recorded on the German North Sea coast by Caspers near Cuxhaven, and in 1947 by Ellenby from Blyth, Northumberland. It is now widespread along the English south coast in *M. edulis*, but the distribution still shows some irregularities that are discussed in this paper.

I am grateful to Prof. J. E. G. Raymont for facilities at University College, Southampton, and for the use of a research table at Plymouth; to Mr F. S. Russell, F.R.S., and the staff of the Plymouth Laboratory of the Marine Biological Association for their assistance; and to Dr D. P. Wilson for facilities to collect at Exmouth. Dr H. A. Cole and Mr J. N. R. Grainger have kindly given me information from their papers not yet published. Dr D. J. Crisp and Dr H. G. Stubbings have assisted by sending me several samples of mussels, and I am grateful also for information received from several other friends named in the text.

## DESCRIPTION

Steuer's description includes the following points. Length: male about 4 mm., female about 8 mm. Body elongated and worm-like. Thoracic segments with paired dorsal processes. Segmentation of abdomen incomplete. Genital openings paired, female carrying two long, narrow egg-sacs, in which eggs are arranged with some regularity. These features are shown in Fig. 1. The head carries a median eye, first antennae of four joints, and second antennae of three joints, the last forming a hook. Lateral to the maxillary base Steuer notes the presence of a soft pocket in the body wall receiving the tip of the antenna. I am unable to recognize this as a permanent structure.

The nomenclature of the mouthparts given by Steuer (1902) was revised by him (1905), when he recognized the opening of the shell gland (excretory gland), but he continued to follow Claus's older work and named the appendage with the excretory gland as 1st maxilliped. Claus (1895) had agreed with Giesbrecht and Hansen to call this appendage the maxilla, preceded by a maxillule and followed by maxillipeds. Wilson (1910) confirmed this arrangement for the parasitic types.

Dollfus (1932) followed Wilson in the main terminology, but criticized the identification of the mandibles by Steuer. It is clear that *Mytilicola* lacks one of the characteristic pairs of appendages, and Steuer thought this to be the post-mandibular pair. Dollfus, by a comparison with *Lichomolgus*, *Ergasilus*, *Panaietis* and *Trochicola*, has shown that in all probability the mandibles are lost and the first mouthparts present are the maxillules. My examination of the larval stages supports Dollfus's conclusion (see below, and Fig. 3).

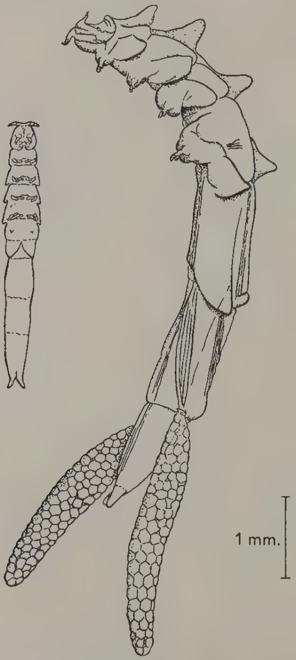

Fig. 1. *Mytilicola intestinalis*, adult male (left) from the ventral aspect, and female (right) with egg-sacs in left dorso-lateral view. The dorso-lateral processes are shown, by which the animal presses the ventral surface with appendages against the opposite wall of the host's intestine.

My interpretation of the head of the female is shown in Fig. 2A. Whole specimens have been mounted direct in polyvinyl lactophenol and lignin pink, and also dissections have been made with the Labgear Harding micromanipulator. The base of the maxillule is deeply embedded in the head, and the projecting part fits closely in a depression of the anterior margin of the maxillary base. The maxillules are wide apart, and their movements contribute only slightly to the feeding process. They may assist in movement through the gut of the host, or in maintaining a hold while the antennae are released and moved forward.

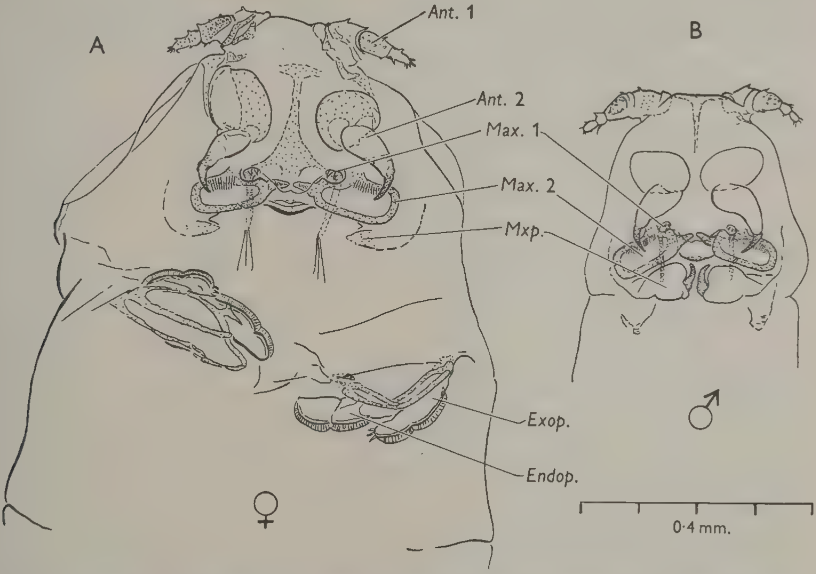

Fig. 2. *Mytilicola intestinalis.* A, head and first free thoracic segment of a mature female. B, the head of a male, in ventral view. *Ant.* 1, antennule; *Ant.* 2, antenna; *Max.* 1, maxillule; *Max.* 2, maxilla; *Mxp.*, maxilliped, vestigial in the female. In both sexes the upper and lower lips are shown, the former covering the inner ends of the maxillae. *Exop.*, exopodite, and *Endop.*, endopodite of the typical thoracic limb.

The base of the maxilla is thickly sclerotized. On the posterior border it carries the aperture of the excretory gland. The inner side of the base carries a pointed projection bearing minute serrations. This part of the maxilla meets its counterpart of the opposite side and is used to push food into the mouth. As noted above, the anterior margin of the maxilla is hollowed around the maxillule, and lateral to this it bears a row of ridges which lie adjacent to the hook of the antenna. Each ridge projects at its posterior end, forming a small tooth. It appears that these structures also assist in maintaining position in the host. Behind the maxillae is a pair of quite vestigial maxillipeds.

The upper lip is a well-defined structure, overlapping the inner processes of the maxillae. The lower lip is less prominent, but it forms a firmly sclerotized line between the maxillary bases.

In the male, Fig. 2B, the head appendages follow closely the structure described for the female. The maxillipeds are, however, well developed. Each has a large swollen base, and a strong hook curved in a forward direction.

The first four pairs of thoracic feet are similar in both sexes. The base is a double chitinous ring, carrying exopodite and endopodite each of two joints. Their outer edges carry a ridge of thin cuticle with some vertical striation which may easily be mistaken for fine hairs. A few small spines and bristles occur on each foot. The fifth pair of feet are reduced to short bristled pegs.

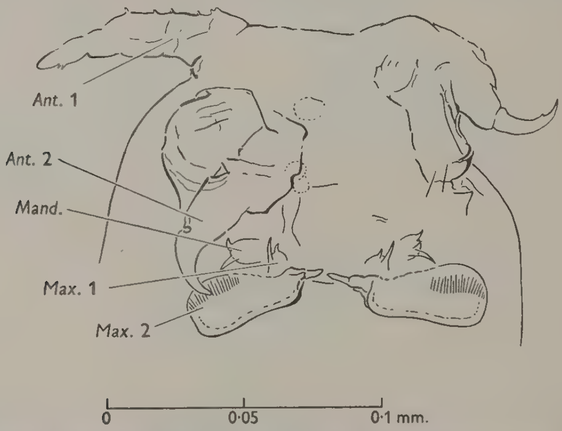

Fig. 3. *Mytilicola intestinalis*, head of a larva of the second parasitic instar, showing the mandible (*Mand.*) which is subsequently lost. The relationship between the maxillule (*Max.* 1) and maxilla (*Max.* 2) is very similar to that of the adult.

## HABITAT AND LIFE HISTORY

The worm-like parasites lie in the recurrent intestine or rectum of *Mytilus edulis*, but not in the direct intestine or style sac. Generally they have a bright red colour and are easily seen, but occasionally quite active individuals are found with no colour. The female parasite occupies most of the lumen of the gut and presses the ventral surface close against the wall with the aid of the paired dorsal thoracic processes. Between these processes the main stream of the host's food is allowed to pass. In the intact gut I have seen little activity, but as soon as contact with the gut wall is lost the parasite begins vigorous peristaltic contractions. If only the posterior half is exposed the parasite can quickly crawl farther into the gut, but when fully exposed its power of locomotion is greatly reduced. At such times a frequent upward flick of the head is noticed, and it is probable that such a movement in the normal environment would ensure that some of the food mass passed to the oral surface of the parasite. Adult females appear to be always orientated with the head towards the oncoming food, but the smaller males seem to move about more freely. Probably the male maxilliped is used in pairing. Despite the large numbers of fresh specimens examined, pairing has never been observed, and it is safe to assume that the association is quite temporary.

When a group of mussels is kept in the laboratory for 2 or 3 days the parasites may move down the gut until the egg-sacs protrude from the anus, but no adult parasite has been seen to leave the host. Females may be found with the eggs in various stages of development, but they are seldom found with eggs ready to hatch. Parasites removed from the host may retain the egg-sacs even after all the eggs have hatched, but they are easily detached at any stage. It seems probable that only mechanical forces in the host gut cause the shedding of egg-sacs, and this not long before hatching.

The youngest egg-sacs, with an opaque pink colour, were removed and cultured in beakers containing 150 c.c. Plymouth 'outside' sea water. No special filtration or sterilization of the water was found necessary. Slow aeration was maintained and the larvae were fed with cultured *Chlamydomonas*. The average temperature was 18° C.

Under these conditions the embryos develop a translucent brown tint, with a prominent red eye in each. Hatching occurs in about 7 days, and the nauplius and metanauplius instars are passed on the eighth day. These two larvae show a strong positive phototropism, which was seen by all previous workers, who also noted that the reaction is lost at the third instar (1st copepodid). The copepodid is an active swimming stage with two pairs of biramous thoracic limbs. Its movement in culture vessels is occasional or spasmodic, and since it is markedly more dense than the water, it tends to swim in the lower part of the vessel. This may be important among factors limiting the distribution.

The first copepodid is the infective stage, and although Pesta (1907) failed in his efforts to infect mussels, Caspers (1939) and Grainger (private communication) found no difficulty. The present author has reared many larvae, and carried out the infection of a mussel measuring 11 mm. long. From this host twenty-two fourth- and fifth-instar parasites were recovered after 3 weeks. This probably does not reflect a normal growth rate, for such a heavy infection of a small host is unusual, and the copepodids may have had only a minimum of food.

Caspers figured three parasitic instars before the adult form, and no attempt has been made here to check his observations. Dollfus has noted that previous figures of the larvae do not show the detail needed to decide the fate of the mandible and maxillule. I have examined all the earlier larvae, and Fig. 3 shows the head of a fifth-instar (second parasitic) larva. Although their cuticle is but slightly thickened, it is possible to discover at this stage both pairs of appendages, and therefore to confirm that the mandible is the appendage missing from the adult head.

## DISTRIBUTION

Altogether over a thousand mussels have been examined, by opening the whole intestine of each specimen, from sites extending from Kent to Cornwall. In the neighbourhood of Southampton mussels have been examined at all times of the years 1948–50, and no significant seasonal variation was detected. On each occasion females with egg-sacs were present. Males were always the more numerous, a typical sample yielding 182 males: 53 females. Larval stages were seldom found. Although some may have been overlooked because of their small size, I believe it is safe to infer that the time occupied by the three larval parasitic instars is short when compared with the average span of adult life.

In many places it was difficult to secure an adequate sample of mussels, but Table I shows that the absence of the parasite cannot be assumed at any of these sites.

Further reports have been received, and are gratefully acknowledged as follows:

Whitstable, Kent, the parasite is common (Dr G. E. Newell)
Littlehampton, Sussex, mussels are not numerous but the parasite is present (Mr E. W. Baxter)
Poole Harbour, Dorset, very abundant 1950 (Dr H. A. Cole)
Falmouth Harbour, Cornwall, present 1949 (Dr H. A. Cole)
Teignmouth, Devon, absent 1949 (Dr H. A. Cole)
Fowey, Cornwall, absent 1949 and 1950 (Dr H. A. Cole)
Conway, Caernarvonshire, absent (Dr H. A. Cole)
Co. Cork, Eire, the parasite is common (Mr J. N. R. Grainger).

## DISCUSSION

### *Estuarine and Marine Environments*

Caspers has suggested that the parasite may be indicative of polluted water, being particularly prevalent in the shallow waters of estuaries. He does not give a detailed description of his sites, but Neuharlingersiel and Karolinensiel would appear from the map to be protected shallows and not true estuaries, and these areas he found to be heavily infested. Other areas such as Norddeich and Busum appear to be similar, yet the parasite was absent. From all the more exposed situations and deeper waters he obtained no *Mytilicola*. The density of the population in the infected areas led Caspers to suppose that the parasite was not a recent immigrant, but had been previously overlooked.

Ellenby, reporting a heavy infestation at Blyth in 1946, was convinced that the parasite was newly arrived, for mussels had been regularly examined from that area over a period of some years. The same experience obtains at Southampton, where the Woolston mussels were at least relatively free until 1948. Seventy parasites were then recovered from twenty-four hosts in a sample of thirty-nine mussels. This density of population shows that the parasite is able to establish itself rapidly in the muddy and often shallow waters of harbours and estuaries. It is unlikely that such an obvious parasite would have been overlooked for long at Plymouth, yet the mussels now in the Tamar and Lynher estuaries show an average of eleven parasites per host.

TABLE I. SOUTH COAST DISTRIBUTION OF *MYTILICOLA INTESTINALIS*

| Locality | No. of *Mytilus* opened | No. infected | Type of site and remarks |
|---|---|---|---|
| Birchington, Kent | 18 | 9 | Mussel bed offshore |
| Bognor, Sussex | 16 | 10 | Open shore |
| Langstone Bridge, Hayling Island | 5 | 4 | Attached to stones in mud; protected |
| Horsey Island, Portsmouth Harbour | 5 | 1 | Attached to stones in wall; protected |
| Sandown, Isle of Wight | 19 | 12 | Low down on pier. Flat shore. |
| Titchfield, Hants | 78 | 60 | Mussel bed offshore, protected by island |
| Hook Bungalow, Hants | 9 | 9 | Stones on flat shore |
| Woolston, Southampton (River Itchen) | 39 | 24 | On pier and from the ground; estuarine |
| Eling, Southampton (River Test) | 50 | 19 | Wreck on muddy bottom near L.W. |
| Milford-on-sea, Hants | 8 | 6 | On groynes; exposed |
| Barton-on-sea, Hants | 5 | 0 | On groynes; exposed |
| Mudeford, Christchurch (River Avon) | 45 | 16 | Concrete blocks on shore |
| Sandbanks, Poole Harbour | 3 | 2 | Protected |
| Studland Bay, Dorset | 13 | 13 | On low rocks |
| Exmouth, Devon: | | | |
| (*a*) On quay wall | 50 | 0 | Vertical surface, strong current |
| (*b*) Bull Hill Bank | 100 | 1 | Extensive mussel bed in estuary |
| Goodrington Sands, Paignton | 36 | 2 | From flat rocks among sand |
| Brixham, Devon: | | | |
| (*a*) On floating pontoon | 134 | 13 | From sides and under |
| (*b*) On sea bed | 18 | 1 | Few mussels only under rocks |
| Steer Point, River Yealm, Devon | 50 | 46 | Very protected bed in estuary |
| Cattewater, Plymouth | 113 | 4 | In cracks of quay wall. Protected and estuarine |
| Plymouth Sound: | | | |
| (*a*) Rum Bay | 23 | 1 | On rocks near H.W. |
| (*b*) Pier piles | 107 | 5 | All on nearly vertical surfaces |
| (*c*) Drake's Island | 50 | 1 | |
| (*d*) Promenade wall | 15 | 1 | |
| (*e*) West Hoe | 20 | 1 | |
| Neal Point, River Tamar | 77 | 70 | Specimens dredged in estuary |
| Anthony Quay, River Lynher | 53 | 49 | From stones in mud. Protected estuary |
| Cawsand Bay, Cornwall | 20 | 0 | Small specimens on rocks near H.W. |

Ellenby noted that the mussels of the only bed of purely marine character available in his area, at Holy Island, contained no *Mytilicola*. This agreed with

Caspers's observations. The records given here show that *Mytilicola* is quite capable of parasitizing mussels of a purely marine environment, either on open shores (Bognor, Sandown, Studland), or in more protected places (Titchfield). In fact from all the marine areas examined negative results were obtained only at Barton-on-Sea, Hants, and Cawsand Bay, Cornwall. At the former site the sample was obviously inadequate, and *Mytilus* was itself barely established on the shore. At Cawsand the mussels were better established, but they were not numerous and individuals were somewhat stunted in growth.

Whatever factors may limit the distribution of *Mytilicola intestinalis*, the species is not restricted to estuarine environments, although these may provide optimum conditions for its growth. In view of the power of rapid colonization here shown, it seems likely that those few estuaries that remain free will not for long maintain their immunity.

### *The Invasion of New Areas*

Established beds of *Mytilus edulis* may become parasitized in either of two ways. First, by the larvae of *Mytilicola* being distributed by tidal and other currents. Secondly, by the introduction of adult or post-metamorphic *Mytilus* which are already parasitized.

The range over which the first method may operate will be limited by the period of free larval life, which appears to be short. If the observations made here are reliable as an indication of natural development, the truly planktonic phase lasts only 3 or 4 days and the copepodid larvae then begin to move downward in the water. The total free life is 10–14 days. If during this time the larvae are dispersed to areas with a low incidence of *Mytilus* there may be no effective spreading of the parasite.

All the facts known at present show that only sexual reproduction can occur, and it involves the presence of the two sexes in one host. It may be significant that in the following samples showing a low incidence of infection only a single parasite was recorded in any one host.

| Site | Infected hosts | Total sample |
|---|---|---|
| Cattewater, Plymouth | 4 | 113 |
| Plymouth Sound | 9 | 215 |
| Brixham | 14 | 152 |
| Paignton | 2 | 36 |
| Exmouth | 1 | 150 |

A slightly higher number was found at Mudeford, at the mouth of the Hampshire River Avon where, from a total of forty-five *Mytilus*, sixteen were found to harbour twenty-three parasites. Mudeford is not far away from either Poole Harbour or Southampton Water, either of which could act as a source of infection. No such sources are known in the neighbourhood of either Exmouth, Paignton or Brixham, but the survey of this area is not yet completed and no mussels have been examined from the Dart estuary.

The mussel colonies of the Tamar and Lynher estuaries, Plymouth Sound and the Cattewater show striking differences of infection which call for explanation. In each area quite dense colonies are to be found, though rather less in the Cattewater. Ten mussels taken at random at Anthony Quay (River Lynher) contained 115 parasites of which thirty-nine were females carrying egg-sacs. We might expect the production of larvae from this area to be sufficient to infect rapidly all mussels in the Sound, but this has not yet occurred. In the Lynher and Tamar the mussels are on flat beds of mud and stones; in the Sound all are on steep or vertical surfaces free of mud, and in the Cattewater most of the mussels were taken from crevices in the quay walls and none were found by dredging.

It is suggested that because of the sinking effect in the infective copepodid stage mussels on the bottom are much more susceptible to infection than those raised on steep surfaces. Experiments are now being started at Southampton to test the relative rates of infection of buoyed and bottom-living groups of mussels. The evidence afforded by the material from Brixham is inconclusive, but not encouraging to this hypothesis. From a floating pontoon 134 mussels were examined, and thirteen were infected, each with a single parasite. Very few mussels were to be found on the sea-bed in this area, and only one out of eighteen was infected.

The spreading of *Mytilicola* by introduction of infected *Mytilus* may occur accidentally on driftwood or on shipping, or by the deliberate importation of mussels where they are used for bait. It appears most likely that shipping across the North Sea has introduced the parasite to harbours and estuaries along our eastern and southern coasts, and into Eire. Yet some have remained relatively free (Exmouth and Fowey) which are visited by a moderate amount of coastal traffic, while others (Yealm River) have a heavy infection and little or no shipping. Where *Mytilus* is used either for food or as bait the introduction of specimens from another port would be rash unless it were accompanied by a very careful examination for *Mytilicola*.

## EFFECT UPON THE HOST

Caspers could not find any direct evidence of a harmful effect upon the host, but he records that the rate of filtration of water was reduced. It would be reasonable to suppose that an individual harbouring eight or ten parasites, which are common numbers, must suffer some deprivation of food. Taken as a whole, I have the impression that the parasitized stocks are less well nourished, but I have seen a specimen, apparently in normal condition, that contained a female *Pinnotheres* and twenty-seven *Mytilicola*.

The subject is being investigated at the Fisheries Experiment Station, Conway, and Dr Cole informs me in a personal communication, that where parasites are abundant severe loss of condition followed by death may result.

The numbers of *Mytilus* have been greatly reduced in the Tamar off Neal Point during recent years, but until my observations in 1948 the parasite had not been recorded there. I detect a slight reduction in the *Mytilus* population at Woolston, Southampton, over the last 7 years, but could not attribute this to the parasite. Sections of the infected intestine do not reveal any damage to the tissues.

## SUMMARY

*Mytilicola intestinalis*, a copepod parasite of *Mytilus edulis*, is now widespread along the English south coast.

The mouthparts are redescribed, and the loss of mandibles suggested by Dollfus is confirmed by the discovery of both mandibles and maxillules in the second parasitic larval stage.

*Mytilicola* is a comparatively recent immigrant. It has achieved a very high density of infection in harbours and estuaries, but also occurs in exposed and fully marine situations.

Factors influencing the distribution are discussed, and the infection of further estuarine populations of mussels is considered likely.

Owing to the behaviour of the infective copepodid larvae it is suggested that the parasite may be slow to colonize mussels that are raised above the sea-bed. This hypothesis is to be tested by experiment.

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# ON THE VARIABILITY OF REPLICATE PLANKTON SAMPLES AND SOME APPLICATIONS OF 'CONTAGIOUS' SERIES TO THE STATISTICAL DISTRIBUTION OF CATCHES OVER RESTRICTED PERIODS

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(Text-figs. 1–4)

The variability to be expected in replicate plankton hauls, using several methods of hauling and a number of different nets, has been examined by Winsor & Clarke (1940). Some of the variability is due to true sampling variations, inevitable when discrete entities in suspension are sampled, and some is due to inadequacies of sampling technique. Winsor & Walford (1936) found that the variability of their vertical net hauls could be explained on the basis of a random distribution of the population, the variations being ascribed to variations in the volume of water filtered in successive hauls. They fully realized that the alternative, namely a non-random distribution of the population, was not disproved; but they considered that since widely different organisms showed little difference in variability the evidence was strongly in favour of a random distribution. They did note, however, that agreement between these different organisms was less marked when the numbers caught were large.

Analysis of net data by Barnes (1949*a*) was not at variance with the above hypothesis, agreement with Winsor & Walford's results being quite satisfactory. However, when the volume of water filtered was carefully controlled by the use of a plankton pump the variability was of a similar order and the distribution of $\chi^2$ as well as its relation to sample size was similar (Barnes, 1949*b*). This cast doubt upon the validity of the assumption of a random distribution of population.

Ricker (1937) has examined the variability of catches of fresh-water plankton, and has pointed out that the variance is often greater than the mean and that this is evidence of aggregation of the organisms. This work has been extended by Langford (1938), who compared the mean and variance of a number of hauls taken at one station as well as over an area. He found evidence that some of the organisms were aggregated while others could be considered as randomly distributed. However, only a small number of hauls were examined. Similar work by Southern & Gardiner (1926), Ruttner (1930) and Baldi, Cavalli & Pirocchi (1945) has been done on various fresh-water lakes. The problem is in many ways similar to that of the distribution of individual plants, and there has been considerable progress in this work (see reviews by Ashby, 1936, 1948).

The detailed form of the distribution[1] can be determined if a number of samples are available for the construction of frequency diagrams. In the present paper a modified method of collecting small samples in large numbers is described and this has, for the first time, enabled frequency distributions to be set up for plankton.

One of us (H. B.) would like to take this opportunity of thanking Dr R. A. Robb for many valuable and friendly discussions on statistical matters, and we both wish to thank him and Dr F. J. Anscombe for criticism of this paper.

We also wish to thank Captain Stewart and the crew of the *Calanus* for their assistance in the collection of the samples.

## The Collection and Counting of the Samples

In order to obtain a large number of small samples, in which the volume was accurately controlled, the following procedure was adopted. A series of fourteen matched aspirators was set up in a rack, and underneath the stopcock of each a copper tube 1 in. diameter was fastened to a bar running across the front of the whole series. A piece of fine bolting silk (200 meshes/in.) was held over the base of the tube by means of a 'jubilee' clip. The use of aspirators with a narrow neck enabled an accurate volume to be rapidly taken. The mean volume of the aspirators was 5867 ml. with a standard deviation of 84 ml., and therefore a coefficient of variation of only 1·4 %. In all the experiments water was pumped continuously, one person filling up the aspirators until they overflowed. The tap was then opened and the water filtered through the silk on the copper tube. After rinsing the aspirator with filtered sea water and passing the washings through the copper tube the silk was carefully removed, the plankton washed off into a small bottle or specimen tube and a little formalin added. By employing ten people the whole process was kept more or less continuous during the sampling period. Welch (1948) has recently criticized pump-sampling technique, but his objection, namely that water is drawn from depths other than that nominally sampled, does not apply to these experiments, where only small volumes were taken (for example 720 l. *total* in series I) and where some relative movement of ship and water must have taken place.

At first it appeared probable that a reversed-microscope technique would be most suitable for the examination and counting of the plankton. In the earlier samples, therefore, after allowing the plankton to sediment in the specimen tube and removing the excess water, it was transferred to a small Perspex vessel holding about 40 ml. and allowed to settle for at least 2 hr. before examining with a reversed microscope. When the sample was clean and the animals were undamaged this was satisfactory, but some of the samples had a great deal of detritus and this, concentrated on the restricted area of the bottom, hid the smaller animals. In addition, it was impossible to re-orientate one animal without disturbing a large area of the sample, and if many animals had to be thus moved the whole sample was disarranged.

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[1] 'Distribution' is used throughout in both the statistical and general sense; it is clear from the context which meaning is intended.

With the later samples therefore this reversed microscope technique was abandoned. It was found best to let the plankton settle in the specimen tube and then draw off the overlying water by suction through a tube whose mouth was covered with fine silk, taking care not to disturb the settled plankton, and to wash this out into a small Bogorov-type tray made of Perspex and holding about 8 ml. The plankton was then examined with a dissecting microscope. A number of samples were counted by both methods; when the samples were clean the numbers were the same but when there was much detritus the reversed-microscope count gave a smaller number. Although passage through the pump, on the whole, did not damage the animals appreciably, some of the nauplii had lost their long tail spines (e.g. *Temora* and *Centropages*) and a good many of the *Oithona* copepodites had lost the abdomen. It was then sometimes impossible to assign them to the correct copepodite stage.

Three series of samples have been taken. In the first two series (10 and 11 February 1949) 120 and 300 samples respectively were taken from a single constant depth of 10 m. In the third (3 May 1949) four depths, 1, 5, 8 and 10 m. were sampled (see pp. 252–5). In all the experiments the boat was allowed to drift.

Series I and II were taken at a depth of 10 m. in 60 m. of water, in the channel between the Islands of Cumbrae and Bute (about 4° 55′ W., 55° 47′ N.), there being a distinct tendency during the experiment to drift to the south-east. For several days previous to this the wind speed had averaged 19 m.p.h. and during series I it varied from 10 to 14 m.p.h. from a direction of 300° backing to 290°. There was rather more wind on the following day, 20–25 m.p.h., from direction 290° to 270°. The weather was bright on the 10th, overcast on the 11th. Both these series were collected between 10.30 and 14.00 hr. High tide was 9.28 and 10.38 hr. at Greenock on the 2 days, so that the samples were collected on the ebb tide. During the first two series no observations were made of temperature or salinity. However, the sea-surface temperatures were in the neighbourhood of the winter minimum, between 7·0 and 7·5° C., while the salinity was about 31·5 °/₀₀, these figures being obtained in routine observations at Keppel Pier.

In series III, 400 samples were collected at four depths, 1, 5, 8 and 10 m., the depth at the station being 60 m. The position was somewhat different, slightly to the east of south of Little Cumbrae Island, about 4° 57′ W., 55° 41′ N., the ship again being allowed to drift. The wind had been very light for the preceding days (mean 7 m.p.h.), but during the morning of the 3rd it rose and remained at 15–20 m.p.h. during the experiment, the direction being 200–215°. The sky was overcast throughout. During this series temperature and salinity observations were made, the observations being taken as nearly as possible to correspond with the middle of the period during which any part of the collection was being made. The observations are summarized below (Table I), further reference to them being made later.

TABLE I. TEMPERATURES AND SALINITIES OF POSITIONS SAMPLED IN SERIES III

| | Period | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | i | | ii | | iii | | iv | | v | |
| Depth (m.) | Temp. (° C.) | Salinity (°/oo) | Temp. (° C.) | Salinity (°/oo) | Temp. (° C.) | Salinity (°/oo) | Temp. (° C.) | Salinity (°/oo) | Temp. (° C.) | Salinity (°/oo) |
| 1 | 9·64 | 31·85 | 9·61 | 31·78 | 9·70 | 31·67 | 9·78 | 31·65 | 9·90 | 31·73 |
| 5 | 9·23 | 32·00 | 9·46 | 31·89 | 9·64 | 31·78 | 9·56 | 31·74 | 9·70 | 31·82 |
| 8 | 9·00 | 32·09 | 9·21 | 32·03 | 9·60 | 31·80 | 8·88 | 32·03 | 8·90 | 31·92 |
| 10 | 8·76 | 32·07 | 9·18 | 32·09 | 9·58 | 31·65 | 8·81 | 32·09 | 8·79 | 31·96 |
| Time B.S.T. | 10.15 to 11.03 | | 11.09 to 11.49 | | 11.59 to 13.05 | | 13.13 to 14.01 | | 14.09 to 15.03 | |

## A PRELIMINARY COMPARISON WITH PREVIOUS INVESTIGATIONS

It will facilitate subsequent discussion if the results are considered using the methods of previous workers, and for this purpose only those from the simpler series (I and II) will be used. In previous work (Winsor & Walford, 1936; Barnes, 1949*a*, *b*) comparison has been almost entirely limited to paired hauls (see, however, Winsor & Clarke, 1940). $\chi^2$ has been calculated from such paired catches, and the resultant distribution of $\chi^2$ compared with that expected on a Poisson distribution. Using this method the results from two former sets of data (Barnes, 1949*a*, *b*) and from the present series are compared. For the present series counts of all organisms were used when $n_1 + n_2 > 9$, paired samples being obtained by grouping sets of ten small samples in consecutive pairs.

The results are shown as the distribution of $\chi^2$ and as the relationship of $\chi^2$ to sample size (Tables II and III). In spite of the very great differences in volume of water filtered, several cubic metres with the nets and several hundred litres in the present samples, the results are very similar. The most noticeable feature, as was originally pointed out by Winsor & Walford for their own data, is the very large number of values showing a high $\chi^2$ ($>3·841$) (Table II), and the fact that the larger values of $n_1 + n_2$ contribute largely to this value of $\chi^2$; both features are clearly common to all the collections.

A further point can be considered at this stage. It was emphasized by Winsor & Clarke that in their results the standard deviation of the catches was roughly proportional to the mean, and they therefore use logarithmic values to stabilize the variance in their analyses. In the present series, although not directly proportional, the standard deviation increases roughly linearly with the mean, and strictly a transformation of the type $1/\beta \sinh^{-1}\beta\sqrt{x}$ is more appropriate. However, in view of the arbitrary character of some of the divisions made in considering the results, the more complex transformation was not used, the logarithmic transformation being considered adequate. When both transformations were used on selected parts of the data there was no difference in the conclusions to be drawn.

TABLE II. THE DISTRIBUTION OF $\chi^2$ FOR POISSON (EXPECTED ON A RANDOM DISTRIBUTION) AND NET, PUMP AND PRESENT SAMPLES FOR ALL ORGANISMS

| | Poisson | Nets | Pump | Series I and II, present observations |
|---|---|---|---|---|
| 0–0·0039 | 5 | 4·5 | 5·5 | 5·7 |
| –0·0158 | 5 | 1·5 | 3·6 | 1·6 |
| –0·0642 | 10 | 3·7 | 3·6 | 6·6 |
| –0·148 | 10 | 5·2 | 9·1 | 9·1 |
| –0·455 | 20 | 10·4 | 9·1 | 10·1 |
| –1·074 | 20 | 11·2 | 5·5 | 14·2 |
| –1·642 | 10 | 9·0 | 12·7 | 11·3 |
| –2·706 | 10 | 11·9 | 7·3 | 10·4 |
| –3·841 | 5 | 11·2 | 3·6 | 7·6 |
| >3·841 | 5 | 31·3 | 40·0 | 23·4 |

TABLE III. SUM OF $\chi^2$ BY SAMPLE SIZE (POPULATION DENSITY)

(Numbers in brackets indicate number of samples in each group.)

| $n_1+n_2$ | Net | Pump | $n_1+n_2$ | Series I and II, present observations |
|---|---|---|---|---|
| 5–40 | 128·9 (50) | 8·6 (12) | 10–50 | 197·9 (133) |
| 40–170 | 100·5 (44) | 65·4 (19) | 50–100 | 156·7 (72) |
| 170–400 | 69·1 (19) | 51·7 (7) | 100–150 | 154·1 (35) |
| 400–1000 | 161·5 (9) | 128·7 (11) | 150–200 | 99·5 (23) |
| > 1000 | 1726·2 (12) | 227·7 (6) | 200–250 | 64·8 (12) |
| | | | 250–350 | 64·4 (20) |
| | | | 350–(3029) | 343·2 (23) |

## THE STATISTICAL CONCEPTS USED

The study of variation leads naturally to the concept of frequency distributions in which the frequency of the variable quantity under consideration takes each of its possible values. In plankton sampling the number of organisms is discrete, and therefore the frequency distribution is essentially discontinuous. When there is a relatively small number of organisms compared with elemental units of medium, then with the organisms randomly distributed the sampling distribution is described by Poisson's limit to the Binomial Expansion. The relative frequencies with which the samples will contain 0, 1, 2, ..., organisms is given by the series, $e^{-m}, me^{-m}, \frac{m^2}{2!}e^{-m}, \ldots, e^{-m}\frac{m^k}{k!}, \ldots$, where $m$ is the mean number per sample.

Alternatively one may write, $P(x=k)=\frac{m^k e^{-m}}{k!}$, where $P(x=k)$ denotes the probability that a sample will contain $k$ organisms. Agreement between a theoretical and an experimentally determined distribution may be tested by means of the $\chi^2$ test, and $P(\chi^2)=0{\cdot}05$ will be considered the acceptable limit of significance (the classes are grouped when the expected value is less than 5; the degrees of freedom are $n-2$ for testing Poisson). A supplementary test is to calculate the variance and its ratio to the mean. With a Poisson distribution this ratio is unity and the departure from unity is a measure of dispersion. This ratio has been termed the relative variance by Clapham (1936), but Fisher's coefficient of dispersion (Blackman, 1942) appears a more suitable term. The coefficient of dispersion itself has a distribution, and in order to be significantly different from unity it must be greater (or less) by $2\sqrt{[2n/(n-1)^2]}$, where $n$ is the number of samples. The coefficient of dispersion is sensitive as regards aggregation but it will not detect certain types of skew distribution.

It has been found, particularly by botanists studying the distribution of individual plants, that when a Poisson distribution does not fit their data, there are often too many samples containing no individuals and too few containing one individual when compared with the appropriate Poisson series, and as a result the observed frequency curves sometimes show bimodality. New series comparable with Poisson series have been developed which show this same tendency, such series being originally termed 'contagious' by Pólya (1931). Those developed by Neyman (1939) and Thomas (1949) seem to be particularly suitable for biological work (Archibald, 1948, 1950; Beall, 1940; Barnes & Stanbury, 1951).[1] Both are based on the same fundamental assumption, namely, a random distribution of the groups and a random number per group. The presence of a particular individual in a given region increases the probability of there being other individuals present (hence the term contagious series). Beall, working on insects, found that Neyman's Type A (which is the most easily calculated) is the most generally useful of the three Neyman series, and only Type A will be considered here. When the three types are different Beall showed that passing from Type A to B to C the expectation for the 0-frequency class falls, and for classes immediately after 0 tends to rise and then to fall for all subsequent classes. The Type A series, which was developed with particular reference to the emergence of insect larvae from egg masses, when put into the recurrent form of Beall is[1]:

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[1] For a further discussion of such series see Anscombe (1949, 1950).

$$P(x=0)=e^{-m_1(1-e^{-m_2})},$$

$$P(x=k+1)=\frac{m_1 m_2 e^{-m_2}}{k+1}\sum_{t=0}^{t=k}\frac{m_2^t}{t!}P(x=k-t).$$

The distribution is determined by two parameters $m_1$ and $m_2$ in contrast to the Poisson series which is completely determined by one parameter, the mean. These parameters can be taken to be proportional to the mean number of groups per sample ($m_1$) and to the mean number of individuals per group ($m_2$). They can be estimated from the first and second moments, since

$$m_2=(\mu_2-\mu_1')/\mu_1', \quad m_1=\mu_1'/m_2.$$

Since

$$\mu_2/\mu_1'=m_1m_2/m_1m_2(1+m_2),$$

it is clear that where $m_2$ becomes very small and $m_1m_2$ is finite the distribution approaches Poisson, where

$$\mu_2/\mu_1'=1.$$

Thomas's series, with similar fundamental assumptions, also expresses a contagious distribution. It is given by the following:

$$P(x=0)=e^{-m},$$

$$P(x=k)=\sum_{r=1}^{k}\frac{m^r e^{-m}}{r!}\left[e^{-r\lambda}\frac{\lambda^{(k-r)}r^{(k-r)}}{(k-r)!}\right].$$

The parameter $m$ is the mean number of groups per sample, whilst $1+\lambda$ is the mean number of individuals per group. As before, the parameters are obtained from the first and second moments:

$$\mu_1'=m(1+\lambda), \quad \mu_2=m(1+3\lambda+\lambda^2).$$

Clearly, as $\lambda$ becomes very small the distribution approaches Poisson. Since this series is the sum of the products of two simple Poisson series

$$\frac{e^{-m}m^r}{r!} \quad \text{and} \quad e^{-r\lambda}\frac{\lambda^{(k-r)}r^{(k-r)}}{(k-r)!},$$

the terms can be obtained by interpolation from tables (Pearson, 1948).

The frequency distributions given by both Neyman's and Thomas's series are very similar, as might be expected, since they are based on similar fundamental assumptions regarding the population (Barnes & Stanbury, 1951).

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[1] $P(x)$ denotes the probability that the number of individuals in any one sample is $x$. In applying the $\chi^2$ test, 3 degrees of freedom should be subtracted from the total when dealing with the Neyman and Thomas distributions.

However, from the point of view of interpreting the aggregation mentioned, Thomas's parameters are more useful, since the mean number of groups per sample and the mean number of individuals per group are at once evident.

## THE HAULS OF SERIES I

This was the first series using the new technique and 120 samples were collected in $2\frac{1}{2}$ hr.; improved organization enabled more samples to be taken in the same time in later series.

In this series the dominant organisms were: *Pseudocalanus minutus* (Krøyer), *Microcalanus pygmaeus* G. O. Sars, *Temora longicornis* (Müller), *Oithona similis* Claus (all as nauplii), lamellibranch larvae and small eggs (not identified). A small number of nauplii of *Acartia clausi* Giesbrecht were found.

Since the samples were taken over a considerable period of time it is first necessary to examine the results for possible changes in the population during the period of sampling. For this purpose the samples have been grouped in consecutive sets of fifteen, and the results are shown in Table IV and Fig. 1. It is clear from the figure that the organisms are behaving differently. The lamellibranch larvae and the egg population appear to be constant throughout, but *Pseudocalanus* and *Microcalanus* show a sharp, and *Temora* a less sharp, change at about sample 60, whilst *Oithona* nauplii show a tendency to change somewhat later in the series. The change in population is presumably a change either with time or with distance. There is little evidence to suggest that the change is dependent upon time *per se*, as for example in vertical migration. It is rather to be ascribed to a change in space consequent upon the relative changes between boat and water mass with time.

The above suggestion can be tested by considering the first four sets as replicates belonging to period 1 and the second four to period 2 (corresponding to the change indicated by Fig. 1 at sample 60) and an analysis for *Oithona* nauplii, lamellibranch larvae and eggs is given in Table V.

The mean squares for P and P × S are not significant[1] when tested against the appropriate residual, and one can assume that the same population was being sampled throughout. By contrast a similar analysis of *Pseudocalanus*, *Microcalanus* and *Temora* nauplii is given in Table VI.

With these species, although the P × S interaction is not significant, that is the species were caught in the same proportion in the two periods, the value for P is highly significant.

It seems therefore that two distinct populations of *Pseudocalanus*, *Microcalanus* and *Temora* were sampled during the experiment, the boundary between these two populations being sharply defined. Furthermore, there co-existed constant populations of lamellibranch larvae, eggs and to a large

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[1] It will be assumed throughout that the results and the tests of significance are to apply to these experiments only.

TABLE IV. COUNTS OF ORGANISMS IN SERIES I

| Sample nos. ... | 1–15 | 16–30 | 31–45 | 46–60 | 61–75 | 76–90 | 91–105 | 106–120 |
|---|---|---|---|---|---|---|---|---|
| *Pseudocalanus* nauplii | 7 | 8 | 13 | 17 | 38 | 41 | 33 | 26 |
| *Microcalanus* nauplii | 38 | 41 | 47 | 46 | 101 | 94 | 109 | 70 |
| *Temora* nauplii | 8 | 25 | 16 | 29 | 33 | 55 | 36 | 67 |
| *Oithona* nauplii | 29 | 23 | 20 | 26 | 30 | 28 | 33 | 43 |
| Lamellibranch larvae | 47 | 51 | 35 | 34 | 55 | 43 | 55 | 39 |
| Eggs | 9 | 7 | 11 | 1 | 8 | 9 | 6 | 12 |

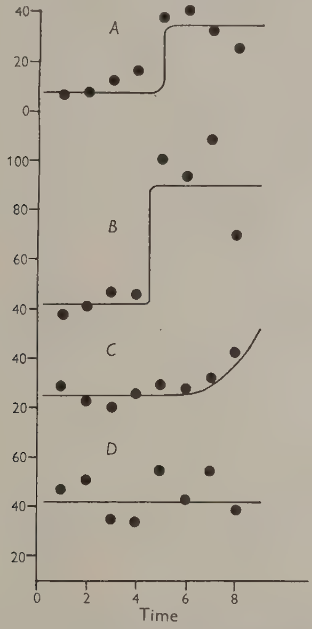

Fig. 1. Counts for repeated hauls, series I, for (A) *Pseudocalanus* nauplii, (B) *Microcalanus* nauplii, (C) *Oithona* nauplii, (D) lamellibranch larvae.

TABLE V

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 1 | 0·1149 | 0·1149 |
| Residual 1 | 6 | 0·2812 | 0·0469 |
| Species (S) | 2 | 2·9845 | 1·4928 |
| P × S | 2 | 0·0244 | 0·0122 |
| Residual 2 | 12 | 0·5329 | 0·0444 |

TABLE VI

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 1 | 1·0583 | 1·0583 |
| Residual 1 | 6 | 0·1939 | 0·0323 |
| Species (S) | 2 | 1·1263 | 0·5632 |
| P × S | 2 | 0·0307 | 0·0154 |
| Residual 2 | 12 | 0·2070 | 0·0173 |

extent *Oithona*. The biological relationship between these populations can be a matter for much speculation. If they have a common origin in a much denser concentration it may mean that one portion of the water mass in which this dense concentration was originally present has maintained its identity to a greater extent or for a longer time than the rest of the water mass. If this were so it is perhaps rather surprising to find extremely sharp boundaries. On the other hand, the two populations may have entirely different origins and may have come together as a result of water movements.

These possibilities might have been tested by a closer examination of the composition of the two populations, for example by size measurements or by finding the proportions of the different nauplius stages, but unfortunately the samples were thrown out before this was realized. The foregoing is based on the idea that the movement of copepod nauplii is dependent on the movement or mixing of water masses. Alternatively, such a mixing of populations may be due to the active movement of swarms of copepods away from denser centres of distribution.

The mean square for P × S is not significant in the analysis for *Pseudocalanus*, *Microcalanus* or *Temora* nauplii, although the value for P is highly significant, that is to say the proportions of the different species did not change significantly although the total numbers changed in the two halves of the experiment. This perhaps adds weight to the suggestion that the populations have a common origin and have become separated by a greater dilution of one portion.

In forming frequency distributions, the populations uniform throughout, namely *Oithona similis* nauplii, lamellibranch larvae and eggs, will be considered first. The frequency distributions and the various parameters are shown in Table VII.

*Oithona similis nauplii*. The coefficient of dispersion is not significantly different from unity and $P(\chi^2)$ for Poisson is 0·2–0·1, indicating an adequate fit to a random distribution. However, there is a clear indication of an excess of the 0-frequency class suggestive of aggregation or clumping, and it is clear from Table VII that both Neyman's and Thomas's series give a better fit to the observed results. From the Thomas parameters the estimated mean number of nauplii per clump $(1+\lambda)$ is 1·1.

*Lamellibranch larvae*. The results are very similar to those for *Oithona*. The coefficient of dispersion and the $\chi^2$ test indicate an adequate fit to a Poisson series. Again the 0-frequency class is high, suggesting aggregation. The Neyman and Thomas series, again similar as would be expected, give a better fit and the mean number per clump as derived from $(1+\lambda)$ is 1·4. It should be noted that the mean is higher than with the previous species, and the increase in the mean is accompanied by an increase in the mean size of the aggregates.

*Eggs*. These small eggs were not identified and belonged to several different organisms and perhaps because of this none of the series gives an adequate fit.

There are an insufficient number of degrees of freedom to test the series but the 0-frequency class, although high, does not appear to be as high as required by contagion.

TABLE VII. SERIES I. ANALYSIS OF FREQUENCY DISTRIBUTIONS OF THE 'UNIFORMLY' DISPERSED FORMS. (120 SAMPLES)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

| | *Oithona similis* nauplii | Lamellibranch larvae | Eggs |
|---|---|---|---|
| Mean | 1·933 | 2·992 | 0·517 |
| Variance | 2·349 | 4·849 | 0·975 |
| C.D. | 1·215 | 1·621 | 1·885 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·260 | 0·260 | 0·260 |
| Ny., $m_1$ | 9·000 | 4·819 | 0·583 |
| Ny., $m_2$ | 0·215 | 0·621 | 0·886 |
| Th., $m$ | 1·736 | 2·204 | 0·336 |
| Th., $\lambda$ | 0·114 | 0·358 | 0·537 |
| $P(\chi^2)$ | | | |
| Pn. | 0·2–0·1 | 0·1–0·05 | $<0·05$ |
| Ny. | 0·5–0·3 | 0·7–0·5 | $<0·05$ |
| Th. | 0·5–0·3 | 0·8–0·7 | $<0·05$ |

| Frequency class | Found | Expected | | | Found | Expected | | | Found | Expected | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Pn. | Ny. | Th. | | Pn. | Ny. | Th. | | Pn. | Ny. | Th. |
| 0 | **23** | 17·4 | 21·1 | 21·1 | **11** | 6·0 | 12·9 | 13·3 | **80** | 71·6 | 85·2 | 85·8 |
| 1 | **28** | 33·6 | 33·0 | 32·8 | **24** | 18·0 | 20·8 | 20·4 | **26** | 37·0 | 18·2 | 16·8 |
| 2 | **34** | 32·5 | 29·3 | 29·1 | **20** | 27·0 | 23·2 | 23·0 | **12** | 9·6 | 9·9 | 10·6 |
| 3 | **17** | 20·9 | 19·2 | 19·1 | **23** | 26·9 | 20·7 | 19·9 | **0** | 1·7 | 4·2 | 4·3 |
| 4 | **8** | 10·1 | 10·2 | 9·9 | **17** | 20·1 | 15·9 | 15·9 | **0** | 0·1 | 1·6 | 1·6 |
| 5 | **7** | 3·9 | 4·7 | 4·2 | **11** | 12·0 | 11·0 | 11·4 | **1** | — | 0·5 | 0·6 |
| 6 | **3** | 1·6[1] | 2·5[1] | 3·8[1] | **5** | 6·0 | 6·9 | 7·3 | **0** | — | 0·4 | 0·2 |
| 7 | — | — | — | — | **4** | 2·6 | 4·1 | 4·2 | **1** | — | — | 0·1 |
| 8 | — | — | — | — | **3** | 1·0 | 2·3 | 2·3 | — | | — | — |
| 9 | — | — | — | — | **1** | 0·3[1] | 1·2 | 1·2 | — | — | — | — |
| 10 | — | — | — | — | **0** | | 0·6 | 0·6 | — | — | — | — |
| 11 | — | — | — | — | **0** | | 0·3 | 0·3 | — | — | — | — |
| 12 | — | — | — | — | **1** | | 0·1[1] | 0·1[1] | — | — | — | — |
| 13 | — | — | — | — | — | — | — | — | — | — | — | — |
| 14 | — | — | — | — | | — | — | — | — | — | — | — |

[1] In this and all subsequent tables of this kind the last class shown of the expected values is obtained by subtraction and includes any higher frequency classes.

The two remaining species are dealt with in the two periods each with uniform population, the results of the analyses being given in Table VIII.

*Pseudocalanus minutus nauplii* (*samples* 1–60). An excellent fit to a random distribution is obtained and no further comments on this series are necessary.

*Microcalanus pygmaeus nauplii* (*samples* 1–60). The results for this copepod are in excellent agreement with a random distribution, $P(\chi^2)$ for Poisson being 0·9 and the coefficient of dispersion very little different from unity, although the population density is moderately high.

*Pseudocalanus minutus nauplii* (*samples* 61–120). $P(\chi^2)$ with Poisson is 0·1–0·05, but for Neyman and Thomas series it is much higher (0·9), showing a closer agreement and again indicating some aggregation.

*Microcalanus pygmaeus nauplii* (*samples* 61–120). In the second part of this series the population density increased very considerably, and since there is a large number of classes the number in any one class is small. Poisson is not an adequate fit, whilst Neyman and Thomas give $P(\chi^2) > 0·05$. The high population density is accompanied by a higher degree of aggregation, the Thomas estimate of the mean number of nauplii per clump being 1·9.

TABLE VIII. SERIES I. ANALYSIS OF FREQUENCY DISTRIBUTIONS OF *PSEUDOCALANUS* AND *MICROCALANUS*

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

| | Samples 1–60 | | Samples 61–120 | |
|---|---|---|---|---|
| | *Pseudocalanus minutus* nauplii | *Microcalanus pygmaeus* nauplii | *Pseudocalanus minutus* nauplii | *Microcalanus pygmaeus* nauplii |
| Mean | 0·750 | 2·867 | 2·300 | 6·233 |
| Variance | 0·801 | 3·304 | 3·671 | 14·419 |
| C.D. | 1·068 | 1·152 | 1·596 | 2·314 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·371 | 0·371 | 0·371 | 0·371 |
| Ny., $m_1$ | — | — | 3·858 | 4·745 |
| Ny., $m_2$ | — | — | 0·596 | 1·313 |
| Th., $m$ | — | — | 1·715 | 3·364 |
| Th., $\lambda$ | — | — | 0·341 | 0·853 |
| $P(\chi^2)$ | Pn., 0·7–0·5 | Pn., 0·9 | Pn., 0·1–0·05<br>Ny., 0·95–0·90<br>Th., 0·98–0·95 | Pn., <0·05<br>Ny., 0·2–0·1<br>Th., 0·2–0·1 |

| Frequency class | Found | Expected Pn. | Found | Expected Pn. | Found | Expected Pn. | Expected Ny. | Expected Th. | Found | Expected Pn. | Expected Ny. | Expected Th. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | **28** | 28·3 | **2** | 3·4 | **11** | 6·0 | 10·6 | 10·8 | **2** | 0·1 | 1·9 | 2·1 |
| 1 | **23** | 21·3 | **12** | 9·8 | **13** | 13·8 | 13·5 | 13·1 | **3** | 0·7 | 3·1 | 3·0 |
| 2 | **6** | 8·0 | **14** | 14·0 | **13** | 15·9 | 12·5 | 12·5 | **6** | 2·2 | 4·7 | 4·7 |
| 3 | **2** | 2·0 | **15** | 13·4 | **8** | 12·2 | 9·5 | 9·4 | **5** | 4·7 | 5·8 | 5·7 |
| 4 | **1** | 0·4 | **9** | 9·6 | **7** | 7·0 | 6·3 | 6·3 | **6** | 7·3 | 6·4 | 6·4 |
| 5 | — | — | **3** | 5·5 | **4** | 3·2 | 3·7 | 3·7 | **7** | 9·2 | 6·5 | 6·5 |
| 6 | — | — | **2** | 2·6 | **2** | 1·2 | 2·1 | 2·0 | **5** | 9·6 | 6·2 | 6·2 |
| 7 | — | — | **1** | 1·1 | **1** | 0·4 | 1·1 | 1·0 | **8** | 8·6 | 5·6 | 5·7 |
| 8 | — | — | **1** | 0·4 | **1** | 0·3 | 0·7 | 1·2 | **1** | 6·7 | 4·7 | 4·8 |
| 9 | — | — | **1** | 0·2 | — | — | — | — | **2** | 4·6 | 3·9 | 3·9 |
| 10 | — | — | — | — | — | — | — | — | **6** | 2·9 | 3·1 | 3·1 |
| 11 | — | — | — | — | — | — | — | — | **4** | 1·6 | 2·3 | 2·4 |
| 12 | — | — | — | — | — | — | — | — | **0** | 0·8 | 1·7 | 1·8 |
| 13 | — | — | — | — | — | — | — | — | **3** | 0·4 | 1·3 | 1·3 |
| 14 | — | — | — | — | — | — | — | — | **0** | 0·1 | 0·9 | 0·9 |
| 15 | — | — | — | — | — | — | — | — | **2** | 0·5 | 1·9 | 1·5 |

## THE HAULS OF SERIES II

This series was taken on the day following series I, at the same depth, and the abundant species were the same. The total time of sampling was $3\frac{1}{2}$ hr., somewhat longer than in series I, but a total of 300 samples was taken. The values for *Pseudocalanus*, *Temora* and *Oithona* are shown in Table IX, in which, since the numbers in any one sample were very small, they have been grouped into ten periods with paired sets of fifteen samples in each period. The analysis of Table IX is given in Table X.

TABLE IX. SERIES II. RESULTS FOR THREE ABUNDANT SPECIES

| Period ... | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | | 9 | | 10 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudocalanus* nauplii | 17 | 25 | 14 | 22 | 32 | 40 | 28 | 27 | 24 | 28 | 29 | 23 | 14 | 17 | 21 | 22 | 8 | 13 | 21 | 14 |
| *Temora* nauplii | 22 | 41 | 28 | 32 | 51 | 49 | 44 | 62 | 63 | 45 | 62 | 48 | 45 | 60 | 72 | 56 | 40 | 65 | 95 | 72 |
| *Oithona* nauplii | 31 | 33 | 22 | 26 | 15 | 50 | 26 | 38 | 16 | 25 | 21 | 24 | 27 | 26 | 19 | 22 | 19 | 26 | 29 | 33 |

TABLE X

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 9 | 0·2877 | 0·0320 |
| Residual 1 | 10 | 0·2081 | 0·0208 |
| Species (S) | 2 | 1·6100 | 0·8050 |
| P × S | 18 | 0·5670 | 0·0315 |
| Residual 2 | 20 | 0·1755 | 0·0088 |

The P × S mean square is significant and one cannot assume that the whole population was constant throughout the sampling period. The population of *Oithona* nauplii appears, however, to be uniform and the analysis confirms this suggestion. Table IX suggests that the populations of both *Pseudocalanus* nauplii and *Temora* also are uniform between periods 3–8 inclusive, and this is confirmed by analysis.

The population with respect to the three species appears to be uniform between 1 and 2 as indicated by Table XI.

TABLE XI

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 1 | 0·0130 | 0·0130 |
| Residual 1 | 2 | 0·0538 | 0·0269 |
| Species (S) | 2 | 0·0890 | 0·0445 |
| P × S | 2 | 0·0078 | 0·0039 |
| Residual 2 | 4 | 0·0207 | 0·0052 |

The results for *Microcalanus* (Table XII) include nauplii and copepodite stages, and inspection suggests that three populations were sampled during the experiment. The numbers were moderately large, and for analysis they may be grouped in paired sets of ten for fifteen separate periods. When all the developmental stages of this species are considered the analysis of variance is shown in Table XIII.

The value for P × St is significant, indicating that the proportion of the stages changed during the experiment. Further, the highly significant value for periods indicates significant changes in the total *Microcalanus* population.

The indication that three populations were sampled has been tested by analysis of the three sections. Analysis of the first section of nauplii and copepodite stages I and II (periods i–v) is shown in Table XIV.

TABLE XII. SERIES II. RESULTS FOR *MICROCALANUS* NAUPLII, AND STAGES I AND II COPEPODITES

Initial section of hauls

| | i | | ii | | iii | | iv | | v | |
|---|---|---|---|---|---|---|---|---|---|---|
| Nauplii | 76 | 153 | 167 | 145 | 171 | 154 | 126 | 165 | 213 | 146 |
| Stage I | 27 | 18 | 19 | 23 | 30 | 16 | 11 | 14 | 29 | 25 |
| Stage II | 29 | 29 | 34 | 37 | 24 | 10 | 17 | 20 | 29 | 34 |

Central section of hauls

| | vi | | vii | | viii | | ix | | x | | xi | | xii | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nauplii | 168 | 115 | 106 | 84 | 86 | 84 | 114 | 80 | 88 | 83 | 98 | 117 | 111 | 83 |
| Stage I | 9 | 5 | 5 | 1 | 2 | 4 | 4 | 2 | 11 | 5 | 2 | 2 | 1 | 11 |
| Stage II | 10 | 11 | 4 | 7 | 10 | 5 | 3 | 3 | 5 | 1 | 4 | 6 | 4 | 9 |

Late section of hauls

| | xiii | | xiv | | xv | |
|---|---|---|---|---|---|---|
| Nauplii | 85 | 112 | 141 | 169 | 130 | 99 |
| Stage I | 10 | 19 | 13 | 4 | 2 | 5 |
| Stage II | 18 | 36 | 24 | 23 | 5 | 7 |

TABLE XIII

| Source of variation | Degrees of of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 14 | 6·5243 | 0·4660 |
| Residual 1 | 15 | 0·8270 | 0·0551 |
| Stages (St) | 2 | 25·9737 | 12·9869 |
| P × St | 28 | 2·6901 | 0·0961 |
| Residual 2 | 30 | 1·1141 | 0·0371 |

TABLE XIV

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 4 | 0·1802 | 0·0451 |
| Residual 1 | 5 | 0·1031 | 0·0206 |
| Stages (St) | 2 | 4·5074 | 2·2537 |
| P × St | 8 | 0·1953 | 0·0244 |
| Residual 2 | 10 | 0·1078 | 0·0108 |

The value for neither P × St nor the periods is significant, and it can therefore be assumed that the population as regards these stages was uniform in the first five periods.

The analysis for periods vi–xi, grouping into three sets since stages I and II are few in numbers, is shown in Table XV.

Again a uniform population can be assumed.

It will be remembered that P × St was significant for three developmental stages. However, if only copepodite stages I and II are considered this distinction disappears as seen in Table XVI, although the value for P still remains significant.

The proportions of stage I to stage II therefore remained the same although the totals changed.

The other organisms present in quantity were lamellibranch larvae, and inspection of the results suggests considerable variability at the beginning and towards the end of the experiment. However, analysis indicates the central section to be uniform (Table XVII).

TABLE XV

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 2 | 0·0971 | 0·0486 |
| Residual 1 | 3 | 0·1450 | 0·0483 |
| Stages (St) | 2 | 7·3855 | 3·6928 |
| P × St | 4 | 0·0408 | 0·0102 |
| Residual 2 | 6 | 0·2686 | 0·0448 |

TABLE XVI

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 14 | 7·9771 | 0·5698 |
| Residual 1 | 15 | 1·2045 | 0·0803 |
| Stages (St) | 1 | 0·4527 | 0·4527 |
| P × St | 14 | 0·9044 | 0·0646 |
| Residual 2 | 15 | 0·6082 | 0·0405 |

TABLE XVII

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Periods (P) | 11 | 0·2203 | 0·0200 |
| Residual | 12 | 0·1663 | 0·0138 |

The situation is obviously more complex than in series I and the division by inspection in the first instance arbitrary. It will be as well therefore to recapitulate the results of the variance analyses in order to get a clear picture of the component populations.

(i) *Oithona* was uniform throughout. (ii) *Pseudocalanus* and *Temora* were uniform between 1 and 2 and between 3 and 8 at different population densities. (iii) *Microcalanus* nauplii and copepodite stages I and II were uniform from periods i to v and also from vi to xi but at a different population density. (iv) If only *Microcalanus* stages I and II are considered, they were caught in the same proportions throughout although the population density changed. (v) Lamellibranch larvae were uniform in the central section. (vi) There was considerable variation towards the end of the experiment.

The existence of a number of different populations sampled during the experiment is clear and confirms the situation evident in series I. However, there is a distinct tendency towards irregularity at some of the boundaries, which have to some extent been selected in an arbitrary manner. On the hypothesis, suggested in the discussion on series I, that populations may be associated with water masses, one might infer that this variability at the population boundaries was due to the breaking up and mixing of these water masses. Apart from these boundary variations, a tendency towards a division into three populations for all the species considered (except *Oithona*) is reasonable. This suggests that all three have some common origin and, in view of their different biological characters, further strengthens a physical interpretation. There is only limited information on the length of time taken by *Microcalanus* to develop from egg to stage II, but it is probably about a fortnight (see Marshall, 1949). The constancy in the proportions of three developmental stages at two different population densities and of copepodite stages I and II throughout suggests a common biological origin, unless egg production had taken place at the same time and environmental conditions had remained the same in the two different regions sampled.

Using only those populations shown to be uniform the frequency distributions can again be constructed (Tables XVIII, XIX, XX).

*Oithona nauplii—all samples*. The results are shown in Table XVIII. Poisson is a very good fit but even so the 0-frequency class is high and both the contagious series give a higher $P(\chi^2)$ indicating a tendency to aggregation.

*The less abundant species*. An excellent fit [$P(\chi^2) = 0{\cdot}9$–$0{\cdot}8$] to Poisson is obtained, and although the population density is higher than in the other populations where Poisson was a less adequate fit, it should be remembered that this is the distribution of a grouped set of animals, each one of which is at a much lower population density.

*Pseudocalanus nauplii* (*central section*, 3–8). The numbers in the first section are small, and only the central section has been analysed. The results are shown in Table XVIII and Poisson is a very satisfactory fit.

*Temora nauplii* (*central section*). Again only the central section is analysed, and the results are shown in Table XVIII. As with *Pseudocalanus*, a satisfactory fit to Poisson is obtained even though the population density is double.

*Lamellibranch larvae* (*central section*). Again only the central section is used with similar results to those from the two preceding copepod nauplii. No account was taken of different species or size groups, but the larvae were mostly at an early stage of development and comparitively uniform in size.

*Microcalanus nauplii* (*initial and central sections*) The results are shown in Table XIX. The population density is high in both sections, but it is to be noted that the higher population density in the first section is due to a greater number of clumps per sample (8·8 against 5·1) rather than to an increase in the mean number of nauplii per clump (1·852 and 1·889). The Neyman and Thomas series both give a $P(\chi^2) > 0{\cdot}05$.

*Microcalanus copepodite stage I.* This was the only copepod of which stages other than nauplii were taken in numbers sufficient for analysis in the small volume of water selected for these experiments. The results are shown in Table XX. Poisson is a very good fit for the initial section of stage I. For the central section the numbers of stage I and the frequency classes are small, and the $\chi^2$ test is therefore very insensitive, but a tendency to aggregation is clear.

TABLE XVIII. SERIES II. ANALYSIS OF FREQUENCY DISTRIBUTIONS (1)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

| | *Oithona* nauplii (all samples) | Rare species (all together) | *Pseudocalanus* nauplii (central section) | *Temora* nauplii (central section) | Lamellibranch larvae (central section) |
|---|---|---|---|---|---|
| Mean | 1·758 | 0·930 | 1·690 | 3·640 | 2·808 |
| Variance | 2·377 | 1·029 | 1·789 | 4·250 | 3·249 |
| C.D. | 1·352 | 1·106 | 1·059 | 1·168 | 1·157 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·163 | 0·164 | 0·212 | 0·212 | 0·260 |
| Ny., $m_1$ | 4·999 | — | — | — | — |
| Ny., $m_2$ | 0·352 | — | — | — | — |
| Th., $m$ | 1·474 | — | — | — | — |
| Th., $\lambda$ | 0·192 | — | — | — | — |
| $P(\chi^2)$ | | | | | |
| Pn. | 0·3–0·2 | 0·9–0·8 | 0·5–0·3 | 0·5–0·3 | 0·7–0·5 |
| Ny. | 0·5–0·3 | — | — | — | — |
| Th. | 0·5–0·3 | — | — | — | — |

| | | Expected | | | | Expected | | Expected | | Expected | | Expected |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Frequency class | Found | Pn. | Ny. | Th. | Found | Pn. | Found | Pn. | Found | Pn. | Found | Pn. |
| 0 | **62** | 52·0 | 68·5 | 69·2 | **121** | 118·4 | **36** | 33·2 | **7** | 4·7 | **6** | 7·2 |
| 1 | **92** | 91·4 | 84·7 | 84·1 | **109** | 110·1 | **57** | 56·1 | **17** | 17·1 | **24** | 20·3 |
| 2 | **68** | 80·5 | 67·3 | 67·3 | **48** | 51·2 | **37** | 47·4 | **33** | 31·2 | **32** | 28·5 |
| 3 | **45** | 47·2 | 41·7 | 41·9 | **18** | 15·9 | **32** | 26·7 | **39** | 37·9 | **21** | 26·7 |
| 4 | **22** | 20·8 | 22·0 | 22·1 | **2** | 3·7 | **13** | 11·3 | **27** | 34·6 | **17** | 18·8 |
| 5 | **6** | 7·3 | 10·3 | 10·3 | **0** | 0·7 | **4** | 3·8 | **26** | 25·3 | **9** | 10·5 |
| 6 | **4** | 2·1 | 4·4 | 4·4 | **2** | — | **1** | 1·5 | **11** | 15·4 | **7** | 4·9 |
| 7 | **1** | 0·5 | 1·7 | 1·7 | — | — | — | — | **10** | 8·0 | **2** | 2·0 |
| 8 | **1** | 0·1 | 0·6 | 0·6 | — | — | — | — | **7** | 3·6 | **1** | 0·7 |
| 9 | **0** | 0·1 | 0·2 | 0·2 | — | — | — | — | **3** | 2·2 | **1** | 0·4 |
| 10 | **0** | — | 0·1 | 0·1 | — | — | — | — | — | — | — | — |
| 11 | **1** | — | 0·5 | 0·1 | — | — | — | — | — | — | — | — |

*Microcalanus copepodite stage II (central section only).* Here again the numbers and the frequency classes are small but the same tendency as seen in stage I is apparent.

*Microcalanus copepodite stage III (initial section only).* Again with the low population density the numbers and frequency classes are low. However, Poisson gives a fair fit.

TABLE XIX. SERIES II. ANALYSIS OF FREQUENCY DISTRIBUTIONS (2)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

| | *Microcalanus pygmaeus* nauplii | |
|---|---|---|
| | Early section | Central section |
| Mean | 16·330 | 9·600 |
| Variance | 37·759 | 22·664 |
| C.D. | 2·312 | 2·360 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·286 | 0·233 |
| Ny., $m_1$ | 12·450 | 7·060 |
| Ny., $m_2$ | 1·312 | 1·360 |
| Th., $m$ | 8·816 | 5·082 |
| Th., $\lambda$ | 0·852 | 0·889 |
| $P(\chi^2)$ | | |
| Pn. | $<0·05$ | $<0·05$ |
| Ny. | 0·7–0·5 | 0·7–0·5 |
| Th.* | 0·5–0·3 | 0·8–0·7 |

| Frequency class | | Expected | | | | Expected | | |
|---|---|---|---|---|---|---|---|---|
| | Found | Pn. | Ny. | Th. | Found | Pn. | Ny. | Th. |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0·8 | 0·9 |
| 1 | 0 | 0 | 0·1 | 0·1 | 2 | 0·1 | 1·9 | 2·0 |
| 2 | 0 | 0 | 0·1 | 0·2 | 4 | 0·5 | 3·7 | 3·7 |
| 3 | 0 | 0 | 0·3 | 0·3 | 3 | 1·5 | 5·8 | 5·8 |
| 4 | 2 | 0 | 0·6 | 0·6 | 5 | 3·6 | 8·0 | 8·0 |
| 5 | 0 | 0·1 | 1·0 | 1·0 | 8 | 6·9 | 10·0 | 9·9 |
| 6 | 2 | 0·2 | 1·6 | 1·6 | 16 | 11·1 | 11·6 | 11·5 |
| 7 | 0 | 0·5 | 2·2 | 2·2 | 13 | 15·2 | 12·5 | 12·5 |
| 8 | 6 | 1·0 | 3·0 | 3·0 | 12 | 18·2 | 12·9 | 12·9 |
| 9 | 3 | 1·8 | 3·8 | 3·8 | 13 | 19·4 | 12·7 | 12·7 |
| 10 | 2 | 3·0 | 4·5 | 4·5 | 15 | 18·6 | 11·9 | 12·0 |
| 11 | 7 | 4·5 | 5·2 | 5·2 | 15 | 16·3 | 10·9 | 10·9 |
| 12 | 8 | 6·1 | 5·8 | 5·8 | 9 | 13·0 | 9·6 | 9·6 |
| 13 | 4 | 7·6 | 6·2 | 6·3 | 9 | 9·6 | 8·2 | 8·2 |
| 14 | 4 | 8·9 | 6·4 | 6·5 | 7 | 6·6 | 6·8 | 6·9 |
| 15 | 11 | 9·7 | 6·4 | 6·5 | 4 | 4·2 | 5·5 | 5·6 |
| 16 | 6 | 9·9 | 6·3 | 6·5 | 4 | 2·5 | 4·4 | 4·4 |
| 17 | 8 | 9·5 | 6·0 | 6·2 | 6 | 1·4 | 3·4 | 3·4 |
| 18 | 6 | 8·6 | 5·6 | 5·8 | 2 | 0·8 | 2·6 | 2·6 |
| 19 | 4 | 7·4 | 5·1 | 5·4 | 0 | 0·4 | 1·9 | 2·0 |
| 20 | 4 | 6·1 | 4·6 | 4·8 | 2 | 0·1 | 1·4 | 1·4 |
| 21 | 4 | 4·7 | 4·0 | 23·7 | 1 | — | 3·5 | 3·1 |
| 22 | 3 | 3·5 | 3·5 | | — | — | — | — |
| 23 | 3 | 2·5 | 2·9 | | — | — | — | — |
| 24 | 2 | 1·7 | 2·5 | | — | — | — | — |
| 25 | 3 | 1·0 | 2·0 | | — | — | — | — |
| 26 | 1 | 0·7 | 1·6 | | — | — | — | — |
| 27 | 0 | 0·4 | 1·3 | | — | — | — | — |
| 28 | 2 | 0·2 | 1·0 | | — | — | — | — |
| 29 | 1 | 0·1 | 0·8 | | — | — | — | — |
| 30 | 3 | 0·3 | 0·6 | | — | — | — | — |
| 31 | 0 | | 0·5 | | — | — | — | — |
| 32 | 0 | | 0·4 | | — | — | — | — |
| 33 | 1 | | 4·1 | | — | — | — | — |

* Calculated with later frequency classes grouped as shown.

## TABLE XX. SERIES II. ANALYSIS OF FREQUENCY DISTRIBUTIONS

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

*Microcalanus pygmaeus* copepodites

| | Stage I (initial section) | Stage I (central section) | Stage II (central section) | Stage III (initial section) |
|---|---|---|---|---|
| Mean | 2·217 | 0·353 | 0·529 | 0·560 |
| Variance | 2·783 | 0·468 | 0·675 | 0·675 |
| C.D. | 1·255 | 1·325 | 1·276 | 1·205 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·371 | 0·261 | 0·261 | 0·274 |
| Ny., $m_1$ | 8·686 | 1·087 | 1·925 | 2·727 |
| Ny., $m_2$ | 0·255 | 0·325 | 0·275 | 0·205 |
| Th., $m$ | 1·952 | 0·292 | 0·461 | 0·507 |
| Th., $\lambda$ | 0·136 | 0·205 | 0·148 | 0·105 |
| $P(\chi^2)$ | | | | |
| Pn. | 0·7–0·5 | <0·05 | 0·5–0·3 | 0·1–0·05 |
| Ny. | 0·8–0·7 | — | — | — |
| Th. | 0·9–0·8 | — | — | — |

| | | Expected | | | | Expected | | | | Expected | | | | Expected | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Frequency class | Found | Pn. | Ny. | Th. | Found | Pn. | Ny. | Th. | Found | Pn. | Ny. | Th. | Found | Pn. | Ny. | Th. |
| 0 | **8** | 6·5 | 8·5 | 8·5 | **89** | 83·6 | 88·0 | 88·9 | **74** | 70·1 | 74·8 | 75·1 | **67** | 62·3 | 65·7 | 65·7 |
| 1 | **16** | 14·5 | 14·6 | 14·4 | **20** | 29·5 | 22·4 | 21·2 | **32** | 37·1 | 30·1 | 30·0 | **27** | 34·9 | 30·0 | 30·0 |
| 2 | **14** | 16·1 | 14·4 | 14·3 | **8** | 5·2 | 6·5 | 6·9 | **10** | 9·8 | 10·1 | 10·3 | **11** | 9·8 | 9·9 | 10·0 |
| 3 | **9** | 11·9 | 10·5 | 10·5 | **2** | 0·7 | 2·3 | 2·0 | **1** | 1·7 | 2·8 | 2·9 | **4** | 2·0 | 3·4 | 3·3 |
| 4 | **7** | 6·6 | 6·3 | 6·1 | — | — | — | — | **2** | 0·3 | 1·2 | 0·7 | — | — | — | — |
| 5 | **2** | 2·9 | 3·3 | 2·8 | | — | — | — | | — | — | — | — | — | — | — |
| 6 | **4** | 1·5 | 2·4 | 3·4 | — | — | — | — | — | — | — | — | — | — | — | — |

### THE HAULS OF SERIES III

In this series it was hoped to obtain further information both on the frequency distributions of populations and on their vertical relations. The set up was as follows.

Samples were pumped continuously for a period of about 5 hr., during which time the boat was allowed to drift. With the hose at a depth of 1 m., twenty samples were taken as in the previous series. The hose was then lowered to 5 m., and, after washing out with water from that depth, a further twenty samples were collected. This was repeated at 8 and 10 m. The hose was then brought back to 1 m. and the sequence of samples and depths repeated five times. There are therefore four series of depths, twenty samples at each depth, and what may be termed five periods, each period corresponding to a complete vertical set of four depths, giving a total of 400 samples. Each set of twenty samples took about 10–15 min., each period, therefore, 40–60 min. and five periods 200–300 min.; in point of fact the whole series took 5 hr. (less 12 min.). Salinities and temperatures were determined for each depth corresponding to the sets of twenty samples from that depth, (see p. 236). Such a division into periods has, of course, an arbitrary character since changes *may* have been taking place at different depths at different rates. However, it is the most natural grouping that can be adopted.

On this occasion the more numerous species were: *Calanus finmarchicus* (Gunnerus), *Centropages hamatus* (Lilljeborg), *Temora longicornis* (Müller), *Acartia clausi* Giesbrecht, *Oithona similis* Claus, all as nauplii, *Calanus* eggs and lamellibranch larvae. Attention will first be confined to copepod nauplii and eggs.

For the analysis of variance the twenty samples of any set have been grouped into four sets of five which are considered as replicates for the given depth and period. The analysis is shown in Table XXI.

TABLE XXI

| Source of variation | Degrees of freedom | Mean square |
|---|---|---|
| Periods (P) | 4 | 0·4866 |
| Depths (D) | 3 | 0·5532 |
| P × D | 12 | 0·1768 |
| Residual 1 | 60 | 0·0312 |
| Species (S) | 5 | 27·1112 |
| P × S | 20 | 0·1889 |
| D × S | 15 | 0·5616 |
| P × D × S | 60 | 0·0890 |
| Residual 2 | 300 | 0·0147 |

The values for the mean squares indicate a complex situation. If the results are again to be interpreted as applicable to this experiment only, then, when the mean squares are tested against the appropriate residual, they are found to be significant. It is perhaps simpler, under these circumstances, to consider the organisms separately. The mean squares are given in Table XXII, the degrees of freedom of each source of variation being the same throughout. Again for this particular experiment all the mean squares, with few exceptions, are significant. Thus had the catches for, say, *Calanus* nauplii been obtained by drawing a net vertically through the water column from 10 to 0 m. at each period, then a significant difference would have been found between the catches, equivalent to a significant value of P, the summing over depths being done by the technique. Similarly, the significance of D would have been found had horizontal hauls been taken at the appropriate levels over the given periods, the summation again being done by the sampling technique. The significance of the P × D interaction can be illustrated by using the results for *Temora* in a more conventional way. In Fig. 2 the proportions at the various depths are shown as a percentage of the total, the value at each depth being taken to represent a column reaching half-way between that depth and the depth sampled above and below. The change in that proportion as one passes from period to period is clearly evident. In view of the time of day and the shortness of the interval between two consecutive periods it is hardly possible that these changes represent regular vertical migrations of the *Temora* population between 1 and 10 m. throughout the area of which these catches are samples. However, it must be pointed out that similar changes, based on catches expressed as percentages, and taken at intervals not longer than the beginning and the end of this series, have been held to imply vertical migration, although in such work the regularity of the change over longer periods and its correlation with factors such as light intensity strengthen the argument.

TABLE XXII. SERIES III. THE MEAN SQUARES

| Source of variation | Degrees of freedom | *Calanus* nauplii | *Calanus* eggs | *Centropages* | *Temora* | *Acartia* | *Oithona* |
|---|---|---|---|---|---|---|---|
| Period (P) | 4 | 0·3183 | 0·0466 | 0·2978 | 0·4128 | 0·2333 | 0·0975 |
| Depth (D) | 3 | 0·3211 | 0·0499 | 0·2880 | 1·7440 | 0·6520 | 0·3060 |
| P × D | 12 | 0·1129 | 0·0372 | 0·0829 | 0·2525 | 0·0627 | 0·0741 |
| Residual | 60 | 0·0134 | 0·0053 | 0·0155 | 0·0225 | 0·0199 | 0·0286 |

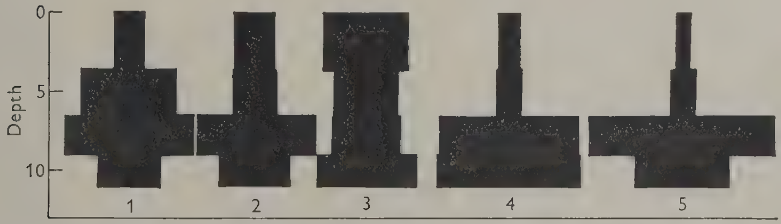

Fig. 2. Data for series III, for *Temora longicornis* nauplii, showing percentage occurrence of total at various depths.

Fig. 3 represents the populations sampled in series III, and salinities are shown in the same type of figure. The salinity samples were taken as far as possible at the mid-point in time of the equivalent set of plankton samples, and the large range of values emphasizes that conditions in this area are not necessarily typical of the open sea.

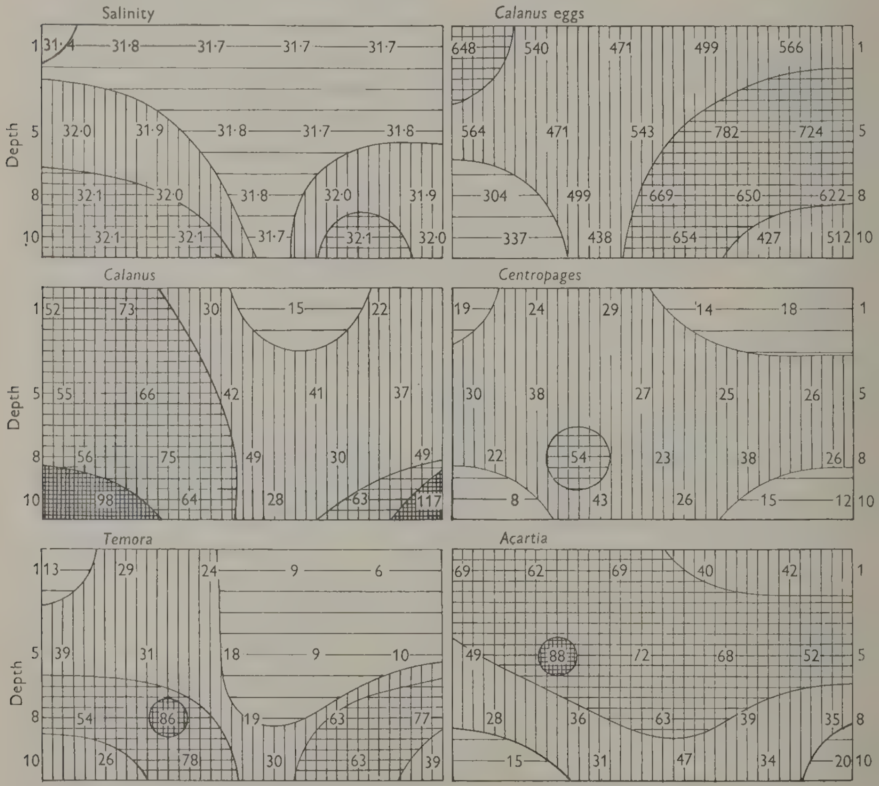

Fig. 3. Population density distributions compared with salinity (top left), for all hauls of series III. Vertical, depth in metres. Horizontal, time (assumed to represent some sort of spatial scale owing to drift). Each diagram shows up to four grades of shading indicating numerically: salinity (°/₀₀), <31·6, 31·6–31·8, 31·8–32·0, >32·0; *Calanus* eggs, <400, 400–600, >600; all nauplii, <20, 20–50, 50–80, >80.

The boundaries of the copepod nauplius populations are again selected somewhat arbitrarily, but they are in the main substantiated by variance analyses which need not be quoted. The arbitrary horizontal axis is a time-scale, but as has already been noted (p. 236) it presumably corresponds with spatial changes in the water.

There is considerable resemblance between all these diagrams, including that for salinity. The regions of high salinity at 8 and 10 m., at the beginning and end of the series, are marked by distinct populations in most of the species, although the relative population density varies according to the species. Thus with *Calanus* nauplii these are regions of high, but with *Centropages* and *Acartia* of low, population density. The population density of these two areas is, however, similar for any one species and had greater depths been sampled in the central period this area might have extended across the figure.

In the third period the low salinity water extends to 10 m., and with *Calanus*, *Temora* and *Centropages* nauplii the populations at all depths during that period are fairly uniform. At the surface, or the surface and 5 m., there is in most species an area of low numbers within the low salinity area.

In general, although the population boundaries are not defined by salinity boundaries, they are most often contained within them; only occasionally does a uniform population spread over a wide range of salinities as it does, for example, for *Acartia* nauplii at 1 and 5 m. and for *Calanus* nauplii during the first two periods.

In several cases the population boundaries are sharp (e.g. *Temora*), but in others there is a suggestion that the nauplii have spread out from one or two centres of high population density. Thus for *Calanus* nauplii there are two apparent centres of distribution in deep water corresponding with high salinity water, and for *Acartia* nauplii one centre at 5 m. from which, although it is situated in low salinity water, the high numbers are spreading out across the boundaries into higher salinity water.

If in the early developmental stages regions of high population density exist, resulting from the production of a large number of eggs, then as time goes on there will be a tendency for these to become dispersed through physical forces, and such information would be essential for a complete interpretation of the figures.

The physical background has been emphasized in suggesting how these populations may be developed, maintained and eventually disseminated, but it must be remembered that the work has dealt mainly with nauplius stages. Clearly with later stages which perform vertical migrations a population could not in this way be restricted to a small water mass. We do not wish to maintain that a given population is always associated with a given mass of water as characterized by its salinity (see above) and it is possible too that a small body of water, apparently homogeneous, may contain separate plankton populations. A large body of water, homogeneous physically by the usually accepted standards, may certainly contain many populations (cf. Baldi *et al.* 1945; Rae & Rees, 1947). However, coincidence of physical conditions and nauplius populations have also been demonstrated above, and it is possible that quite small physical differences which make up what might be termed the 'microclimate' would, on detailed investigation, be found to exist in the regions where those observations were made. It would be interesting to extend this work by trying to follow the history of some of these small zooplankton patches and to apply a similar technique to later developmental stages.

## THE POPULATIONS OF SERIES III

Some of the uniform populations were sufficiently extensive to enable frequency distributions to be formed. Since, however, the results were of very much the same type as those already given, it is not necessary to give them for each population. A selection is given as follows:

TABLE XXIII. SERIES III. ANALYSIS OF FREQUENCY DISTRIBUTIONS

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

| | *Oithona* | *Temora* | *Centropages* 1 | *Centropages* 2 |
|---|---|---|---|---|
| Mean | 1·825 | 1·690 | 5·810 | 5·160 |
| Variance | 2·316 | 1·690 | 9·550 | 5·518 |
| C.D. | 1·269 | 1·000 | 1·644 | 1·069 |
| $2\sqrt{[2n/(n-1)^2]}$ | 0·201 | 0·320 | 0·286 | 0·320 |
| Ny., $m_1$ | 6·784 | — | 9·026 | — |
| Ny., $m_2$ | 0·269 | — | 0·644 | — |
| Th., $m$ | 1·597 | — | 4·232 | — |
| Th., $\lambda$ | 0·143 | — | 0·373 | — |
| $P(\chi^2)$ | | | | |
| Pn. | $<0·05$ | 0·5–0·3 | 0·1–0·05 | 0·3–0·2 |
| Ny. | 0·3–0·2 | — | 0·7–0·5 | — |
| Th. | 0·5–0·3 | — | 0·5–0·3 | — |

| | | Expected | | | | Expected | | Expected | | | | Expected |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Frequency class | Found | Pn. | Ny. | Th. | Found | Pn. | Found | Pn. | Ny. | Th. | Found | Pn. |
| 0 | **42** | 32·2 | 40·4 | 40·5 | **17** | 14·8 | **3** | 0·3 | 1·4 | 1·5 | **0** | 0·5 |
| 1 | **59** | 58·8 | 56·3 | 56·6 | **20** | 25·0 | **3** | 1·7 | 4·2 | 4·2 | **5** | 2·4 |
| 2 | **36** | 53·7 | 46·8 | 46·8 | **22** | 21·1 | **6** | 5·1 | 7·8 | 7·8 | **6** | 6·1 |
| 3 | **34** | 32·7 | 29·5 | 29·6 | **16** | 11·9 | **13** | 9·8 | 10·9 | 10·9 | **15** | 10·5 |
| 4 | **18** | 14·9 | 15·4 | 14·7 | **5** | 7·3 | **10** | 14·2 | 12·9 | 12·8 | **10** | 13·6 |
| 5 | **6** | 5·4 | 7·0 | 5·8 | — | — | **14** | 16·5 | 13·3 | 13·2 | **10** | 14·0 |
| 6 | **5** | 2·2 | 4·6 | 6·0 | — | — | **16** | 16·0 | 12·3 | 12·3 | **8** | 12·0 |
| 7 | — | — | — | — | — | — | **6** | 13·3 | 10·5 | 10·5 | **9** | 8·9 |
| 8 | — | — | — | — | — | — | **10** | 9·7 | 8·3 | 8·4 | **9** | 5·7 |
| 9 | — | — | — | — | — | — | **9** | 6·2 | 6·0 | 6·3 | **8** | 6·3 |
| 10 | — | — | — | — | — | — | **4** | 3·6 | 4·3 | 4·4 | — | — |
| 11 | — | — | — | — | — | — | **2** | 1·9 | 2·9 | 3·0 | — | — |
| 12 | — | — | — | — | — | — | **0** | 0·9 | 1·9 | 1·9 | — | — |
| 13 | — | — | — | — | — | — | **1** | 0·4 | 1·2 | 1·2 | — | — |
| 14 | — | — | — | — | — | — | **2** | 0·2 | 0·7 | 0·7 | — | — |
| 15 | — | — | — | — | — | — | **1** | 0·1 | 1·4 | 0·9 | — | — |

*Oithona.* Here Poisson is not an adequate fit but Neyman and Thomas are a good fit to the data.

*Temora.* Here Poisson is an adequate fit, indicated by a $P(\chi^2)$ value of 0·5–0·3, although again the 0-frequency class is in excess.

*Centropages* 1. The population density is high (5·81), yet Poisson gives an adequate fit. However, the agreement in earlier classes is to some extent the result of grouping.

*Centropages* 2. Here, as with the previous distribution, Poisson is an adequate fit, even though again the population density is high (see p. 261).

## THE SAMPLING VARIATIONS

The results from series I and II are shown in Tables VII, VIII, XVIII, XIX and XX, and the numerical data in the top halves of these tables should be compared. (The number per m.$^3$, if required, is readily obtained by multiplying the mean by 170.) In Fig. 4 the mean population density is plotted against the variance using the values from series I and II. It is clear that as the population density increases the sampling variance increases. If all the populations were randomly distributed then points would be scattered about a line corresponding to mean population density = variance (as indicated in Fig. 4). Only at low population densities is there a close approach to a random

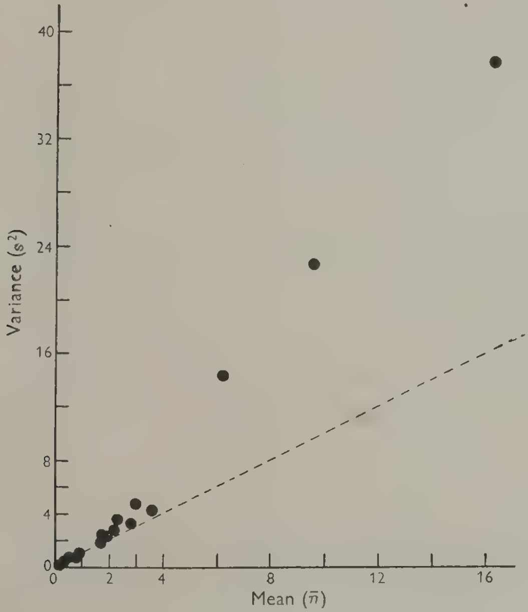

Fig. 4. The relation between the variance ($s^2$) and the mean ($n$) of the populations from series I (Tables VII and VIII) and series II (Tables XVIII, XIX and XX).

distribution. As the population density increases there is clear evidence of aggregation, i.e. the chance of an organism being present is increased by the presence of an organism already there, so that the frequency distributions fit those of a contagious series.

It is now possible to explain the observed distribution of $\chi^2$ in previous work both with nets and pumps. The variation, particularly noted at high population densities, is to be ascribed largely to the greatly increased true sampling variation with increasing population density. As will be discussed later, this change depends to some extent on the biological character and history of the population, but inspection of the above tables shows that in general the Poisson distribution begins to be an inadequate fit when the population density exceeds a value of 1000 organisms per m.$^3$. Now in the early work (Tables II and III) the great change in the mean value of $\chi^2$ begins in the 170–400 $n_1+n_2$ group, increases considerably at the 400–1000 group, becoming very great at the > 1000 group. The change can be taken at somewhere in the region of a population density of 200–300 organisms per sample. In the pump samples about 200 l. of water were taken, so this corresponds to a population density of 1000–1500 organisms per m.$^3$, agreeing with the above calculation. The change can therefore be ascribed largely to sampling variations dependent upon the population sampled, and not to inadequacies in sampling technique. With the net samples the increase in $\chi^2$ began at catches of the same order, and nominally a much larger volume, about 11 m.$^3$, was filtered. The change is therefore taking place at a lower population density than expected. This may in part still be ascribed to errors of technique, such as variations in the volume filtered, but in contrast to a pump haul taken at a single depth it should also be remembered that in a net haul a whole series of populations even of any one organism can be sampled at different levels of the haul, so that the organisms may be concentrated in a relatively small proportion of the volume filtered. Under these circumstances minimal population densities are obtained by the use of 11 m.$^3$ volume.

The preliminary examination of the data indicated that the standard deviation was roughly proportional to the mean. In Fig. 4 the estimated variance is plotted against the mean, and a shallow curve is obtained. The form of the curve and general consideration of heterogeneous distributions (see Anscombe, 1949) suggest that an equation of the following type expresses the relation between variance and mean

$$\sigma^2 = \bar{n} + c\bar{n}^2, \qquad (1)$$

or in a more convenient form as

$$\frac{\sigma^2}{\bar{n}} = 1 + \frac{1}{k}\bar{n}. \qquad (2)$$

There are a number of sets of estimates of $1/k$ (one from each distribution) and

Anscombe has shown that an unbiased estimate of the value for any set, $1/\hat{k}_i$, is given by

$$\frac{1}{\hat{k}_i}=\frac{s_i^2-\bar{n}_i}{\bar{n}_i^2}\left(1+\frac{s_i^2}{N_i\bar{n}_i^2}\right), \tag{3}$$

where $s_i^2$, $\bar{n}_i$ are the estimated variance and mean for the $i$th set, and $N_i$ is the number of samples in that set. The values of $1/\hat{k}_i$ are shown in Table XXIV. There is some variation but no apparent correlation of this value with the mean. (Four high values, one from Table VII and three from Table XX, stand out as somewhat different from the rest, and it is of interest to note that in contrast to the other data, which refer to nauplii, these values are derived from eggs and copepodite stages.)

TABLE XXIV

| Table | Population | Estimated $1/\hat{k}_i$ | Table | Population | Estimated $1/\hat{k}_i$ |
|---|---|---|---|---|---|
| VII | *Oithona* nauplii | 0·112 | XIX | *Microcalanus* nauplii (initial) | 0·080 |
| VII | Lamellibranch larvae | 0·208 | | | |
| VII | Eggs | 1·767 | XIX | *Microcalanus* nauplii (central) | 0·142 |
| VIII | *Pseudocalanus* (1–60) | 0·053 | | | |
| VIII | *Microcalanus* (1–60) | 0·093 | XX | *Microcalanus* copepodites, stage I (initial) | 0·116 |
| VIII | *Pseudocalanus* (61–120) | 0·262 | | | |
| VIII | *Microcalanus* (61–120) | 0·212 | XX | *Microcalanus* copepodites, stage I (central) | 0·949 |
| XVIII | *Oithona* nauplii | 0·201 | | | |
| XVIII | Rare species | 0·115 | XX | *Microcalanus* copepodites, stage II (central) | 0·532 |
| XVIII | *Pseudocalanus* nauplii | 0·035 | | | |
| XVIII | *Temora* nauplii | 0·046 | XX | *Microcalanus* copepodites, stage III (initial) | 0·373 |
| XVIII | Lamellibranch larvae | 0·056 | | | |

Now although an attempt has been made to fit distributions to these populations, an efficient estimate of a common value for the $k$'s can, none the less, be obtained. The method used is equivalent to taking an appropriately weighted average of the separate estimates of $1/\hat{k}$, and $\hat{k}$ is chosen so that it satisfies the equation

$$\Sigma T_i(\hat{k})=0,$$

where

$$T_i(\hat{k})=\frac{(N_i-1)s_i^2-(N_i-1-\hat{k}^{-1})(\bar{n}_i+\bar{n}_i^2/\hat{k})}{(\bar{n}_i+\hat{k})^2}. \tag{4}$$

If the value for eggs (Table VII) is ignored, $1/\hat{k}=0{\cdot}121$; if the high values from Table XX (copepodites) are also ignored the values of $1/\hat{k}=0{\cdot}118$. It is sufficient to take a value of 0·12.

It will be remembered that the equation originally derived from paired observations on the assumption of a random distribution of organisms and variability due to variable volume of water filtered was

$$\chi^2=1+K^2n, \tag{5}$$

where $K^2$ lay between 0·04 and 0·05. For paired observations $\chi^2=s^2/\bar{n}$, and clearly the equation is of the same form as that given above where $K^2 = 1/k$ with an estimated value of 0·12. Now $K$ is not to be regarded as constant, as Winsor & Walford pointed out (they were, for example, not dealing with nauplius stages of copepods, but with a wide variety of organisms), and indeed Silliman (1946) in pilchard egg investigations obtained a value of $K^2 = 0{\cdot}12$, and here the agreement is striking. Now equation (1) was derived from experiment in which the volume of the samples was carefully controlled; the variability can therefore be ascribed to non-random distribution of the organisms (perhaps superimposed on some sampling variation), and it would seem an adequate explanation for Winsor & Walford's results.

## Discussion

In the previous sections some of the features of the animal populations sampled by pump during periods of from 2 to 5 hr. have been considered. The results, however, have a bearing upon plankton work in general, which may now be considered.

Unlike most net catches the volume of water taken in a pump sample is accurately known, being unaffected by many of the factors causing errors in net hauls. Correct estimates of the population are therefore obtained, and these values are readily converted to organisms per m.$^3$, in the present instance, by multiplying by 170. The numbers obtained tend to be larger than those usually reported at this time of the year in this area (Marshall, 1949), which is to be expected since previous estimates have been based on net hauls.

In the present experiments there is no information on the relative movements of ship and water, but the rapid changes in population suggest very strongly the presence of numerous three-dimensional 'swarms' which may be quite small in volume, smaller than those which have been so clearly shown by Hardy & Gunther (1935) for Antarctic plankton, and by several workers for the North Sea, using the continuous plankton recorder (Rae & Rees, 1947). The evidence is in favour of their being restricted laterally and, since the samples of series III were taken at several depths, their vertical limits also are sometimes found to be quite small. If the patterns of Fig. 3 were extended into three dimensions they would give a picture of the situation.

Hitherto most of the work on 'swarms' has been confined to discontinuities in a horizontal direction. Variations in population density in a vertical direction for a given organism are well known, and a movement of these populations is implicit in results which indicate vertical migration. The evidence from the present work relates largely to nauplius stages and these are not known to show diurnal migration. Stress has been laid on the possibility that the 'swarms' are confined in a particular water mass, but if such small 'swarms' exist in the late developmental stages which do show diurnal migration then a similar relation to the water mass would be impossible. If such adult swarms exist and if they preserve their identity during migration some other force must be responsible. This may be a 'positive' biological force such as causes swarming in other animal groups. Since, however, vertical migration is usually considered to be a response to a change in light intensity, and since this acts only in a vertical direction, the movement may occur much more freely in a vertical than a horizontal direction; with a consequent tendency to reduce horizontal dispersion. A repetition of this type of work extended vertically and horizontally and over a longer period is proving of considerable interest.

This evidence, derived largely from a consideration of nauplii, suggests that the distinct populations maintain their identity for some time, and are gradually broken down by physical forces and reduced by mortality as the organisms go through their development. It might be expected, therefore, that copepods which retain their eggs until the nauplii hatch (*Pseudocalanus* and *Oithona* of those here discussed) would, at a given time from hatching, be less widely distributed than those laid singly in the water (the other copepods concerned). There is no evidence about the age from hatching of the nauplii caught, and strict comparisons between the two types cannot therefore be made. It is interesting to observe, however, that in series I the *Pseudocalanus* at a mean population density of 2·300 has a coefficient of dispersion of 1·596, whereas *Microcalanus* with a higher mean population density (2·867) has a coefficient of dispersion of only 1·152. Further, *Temora* in series II with a mean population density of 3·640 and *Centropages* in series III (population density 5·160) have coefficients of dispersion of 1·168 and 1·069, respectively. The results from *Oithona* are in general agreement.

## SUMMARY

A brief review of previous work on the sampling variation encountered in the course of plankton work is given, and leads to the suggestion that the observed variability is not entirely accounted for by technical errors. A non-random distribution (statistical) of the population is suggested.

If the distribution is not random (Poisson) then the application of contagious distributions should be considered. A short account of two such distributions, Neyman's and Thomas's, is given; the parameters of the latter seem to be more readily interpreted in plankton sampling.

An account of the method of collection and counting of numerous small samples taken continuously over several hours is given. In the first two series the collections were made at a constant depth. The results suggest the existence of comparatively well-defined populations of a number of organisms, chiefly copepod nauplii. Series III, in which samples were taken at several depths, confirms this suggestion and indicates a similar state of affairs in a vertical direction. The population changes, it is suggested, might be associated with different masses of water which have maintained their identity over a period during which the populations have been developed, and the association of a number of species maintained.

Frequency distributions are set up, and in general when the population density is low the distribution closely approaches that of Poisson. At higher population densities the Neyman and Thomas series give a better fit, indicating clumping of the organisms. An estimate of the mean number per clump is obtained.

The results are considered in relation to Winsor & Walford's work and it is shown that the sampling variation can be explained as dependent upon the non-random distribution of the organisms sampled. This explanation is adequate for earlier data.

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# AN APPARATUS FOR THE COLLECTION OF PLANKTON IN THE IMMEDIATE VICINITY OF THE SEA-BOTTOM

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(Text-figs. 1–3)

In connexion with a study of plankton-benthos interrelationships off the coast of Northumberland, an apparatus was designed for the collection of plankton in the immediate vicinity of the sea-bottom, a layer usually missed by ordinary plankton sampling gear. The present account is a brief description of this apparatus, together with some notes on its handling at sea and the work carried out with it on board the Dove Marine Laboratory's boat, the *Pandalus II.*

I was fortunate in having the willing co-operation of numerous people who helped in various ways, and to whom I am very greatly indebted. These included my father, Mr E. Bossanyi; Mr T. E. F. Sanderson of Eastcote, Middlesex; Prof. A. C. Hardy, Oxford University; Dr C. E. Lucas, Fishery Laboratory, Aberdeen; Prof. A. D. Hobson, Director of the Dove Marine Laboratory; Dr H. O. Bull, Assistant Director; Messrs Ellis and Co., Engineering Works, Swalwell, County Durham; the Department of Mechanical Engineering of King's College, Newcastle upon Tyne; and the entire scientific, boat and technical staff as well as research students at the Dove Marine Laboratory. Without them, the design, construction and employment of the apparatus would not have been possible.

## Description of the Apparatus

The present apparatus differs from previous designs of bottom-plankton nets (e.g. Russell, 1928; Hardy & Lucas, personal communication), chiefly in being provided with a closing device which operates only by contact with the sea-bottom. It thus eliminates the disadvantage of the earlier designs which necessarily fished both on the way down to and up from the bottom. At the same time, the nature of the closing mechanism avoids the necessity of any extra ropes or cables for messengers etc., and allows the apparatus to be shot rather like a beam trawl from a boat that is slowly moving as well as from a stationary one.

The apparatus is essentially a sledge constructed of tubular steel ($1\frac{1}{4}$ in. diameter) on runners, on which a removable plankton net with bucket is mounted, and bearing in addition two closing doors which fit over the mouth of the net (Figs. 1–3).

The frame consists of two parts, each made in one piece with all joints firmly welded so as to be both strong and waterproof. These are the sledge frame (Fig. 3A), which bears the runners (*u*) and to which the ropes are shackled by means of eyes, and the net frame (Fig. 3B), which is mounted on its vertical bars. This frame can thus move vertically on the sledge frame with a total range of about a foot and can be clamped at any level within this range by wing nuts at (*v*). The actual net with its bucket fits into the net frame, and is fastened at the front end by hooks fitting into perforated steel laths (*w*) on the net frame, whilst at the rear end the bottom of the bucket is fixed to a steel plate (shown in black) by a wing nut. The net frame bears a coarse steel gauze on its lower aspect to protect the net from below, and also the doors, each of which is welded to it by two strong hinges at ($x$, $x'$; $y$, $y'$). All cross-bars of both frames are above the level of the runners.

The net (Fig. 1) is a cone of four sections sewn together, and is constrained into a rectangular shape at its mouth. As in ordinary plankton nets, it has a canvas rim at each end for attachment, achieved, in this net, by means of the hooks already mentioned at the front, and the bucket at the rear.

The bucket (Fig. 1) is constructed on the lines of Hensen's quantitative bucket (Hensen, 1895, pp. 69–71), with a non-filtering lower portion from which there is an outflow (corked during a tow), and a filtering upper portion consisting of the finest bolting silk (200 meshes/in.) which enables the bucket to be used with nets of that or coarser mesh. It is fastened to the net by a threaded rim which screws with a few turns into a ring clamped to the rear canvas of the net. When several nets of different mesh but of the same size and shape are in use therefore, one and the same bucket can easily be fixed to any one net, provided each of these has its own threaded ring clamped to it.

The doors (Fig. 3C) each consist of two steel plates movably bolted to one another. The door proper is permanently welded to the net frame by the hinges already referred to, and closes half of the net mouth-opening. The arm projects out at right angles to the whole apparatus when the door is shut, and its lower end projects 2–3 in. or more below the level of the runners. Because the arm is adjustable relative to the door proper, it can always be kept at this level whatever the vertical position of the net frame in the sledge frame may be. When the apparatus is lowered to the sea-bed and dragged forwards, the lower end of each arm thus digs into the ground and is swept back so as to lie parallel with the frame, thereby opening the doors forwards. The adjustable springs which are attached to the upper margin of the door proper and the upper net frame bar on each side ($z$, $z'$) are extended and put under tension by this action, so that when the apparatus and hence the arms are lifted clear of the bottom, they pull the doors shut. Care was taken in the design to ensure that the areas of door and arm on each side of the points of attachment to the hinges are equal, thus cancelling out to all intents and purposes the effect of water resistance. The only effective forces on the 'open-shut' mechanism therefore are the resistance of the sea-bottom to the arms and the pull of the springs.

The dimensions of the whole apparatus (maximum length 7, maximum width 3, and maximum height 2 ft. approximately), are determined by those of the net it contains. These in turn are determined by two factors: the net must be large enough to obtain a reasonable catch in a short time, and its filtering area must be large enough relative to its mouth area to allow efficient filtering to take place at ordinary plankton net towing speeds (about 1 knot). A consideration of the dimensions of various commonly used nets such as described by Ostenfeld & Jespersen (1924) and Künne (1929, 1933) led to the conclusion that a ratio of 6:1 would in practice meet this requirement, and the present net was made accordingly.

## Handling the Apparatus at Sea

Owing to its considerable weight (about 1½ cwt.) the apparatus cannot be handled without either a derrick or a davit with a winch. Given these requirements, together with a minimum of three people who have learnt the necessary drill for shooting and hauling, the apparatus can be quite comfortably used even in a moderately choppy sea, though in the latter case the steersman must take care to keep the vessel stern into the waves to reduce swaying to a minimum. Two fairly heavy ropes are necessary (2¼ in. circumference), one of which, the lifting rope, is used solely for lowering the apparatus to the bottom and later raising it from just beneath the surface on to the deck, whilst the other, the tow rope, is employed for towing the apparatus along the bottom and hauling in to just below the surface afterwards. With a davit of sufficient height, the apparatus could be hauled in completely by the tow rope and swung in over the deck, hanging in a vertical position. The disposition of the ropes is shown in Fig. 2.

A good deal of information as regards the working of the apparatus when being towed along the bottom could be gleaned from the presence and position of scratch marks on the runners and lower ends of the arms. These parts were therefore often coated with paint sometime before a haul, and scratch marks observed afterwards (see Fig. 2).

## Work done with the Apparatus, 1949–50

The apparatus described here is of course not suitable for use on rocky bottoms. It is doubtful whether any type of sledge arrangement can be used effectively on such grounds. The work carried out with it has been confined to sandy and hard muddy bottoms of which there are great stretches in shallow and deep water off the coast of Northumberland. On these bottoms the apparatus has been found to work very well and a considerable amount of material has been collected with it. It is also planned to use the apparatus on softer muddy

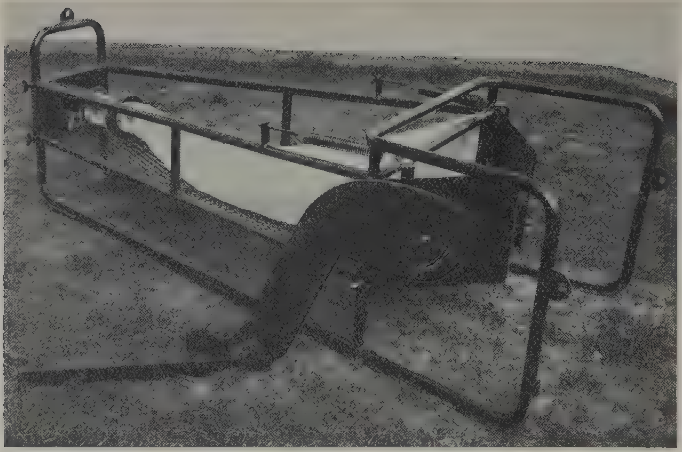

Fig. 1. The whole apparatus assembled with the doors partially opened. The extension on the arm of the door was an experimental addition which proved to be unnecessary.

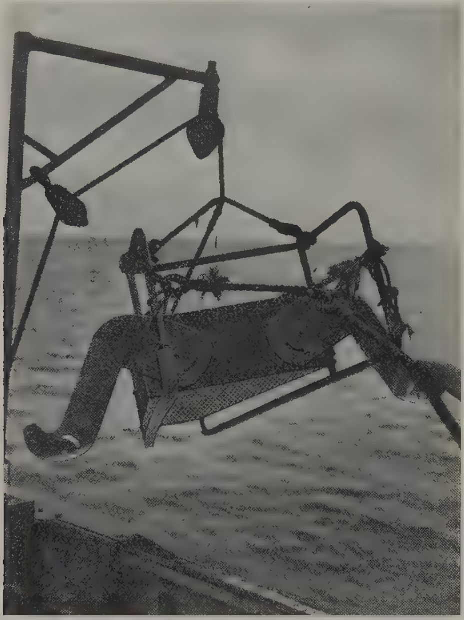

Fig. 2. The apparatus hanging on the davit and about to descend into the sea, showing the davit swung out overboard, and the lifting and tow ropes. Note also the areas scratched clean on the lower ends of the arms during a previous tow.

bottoms, which may present some difficulties owing to its considerable weight, and on shingle and gravelly areas. Collections of plankton above rocky bottoms will have to be tackled by different means, e.g. using a pump and hose, for the smaller species especially. Apart from various trial runs at different places in the initial stages of the work, the apparatus was used fairly regularly with a net of 40 meshes/in. at two stations in the vicinity of Blyth harbour, Northumberland. One of these was in Blyth Bay a few hundred yards offshore in 5–6 fathoms on a sandy bottom; the other in Cambois Bay (north-east of Blyth) in 13–15 fathoms on a bottom of sandy mud. Collections were made at different states of the tide, at different times of the day, and also at night. The

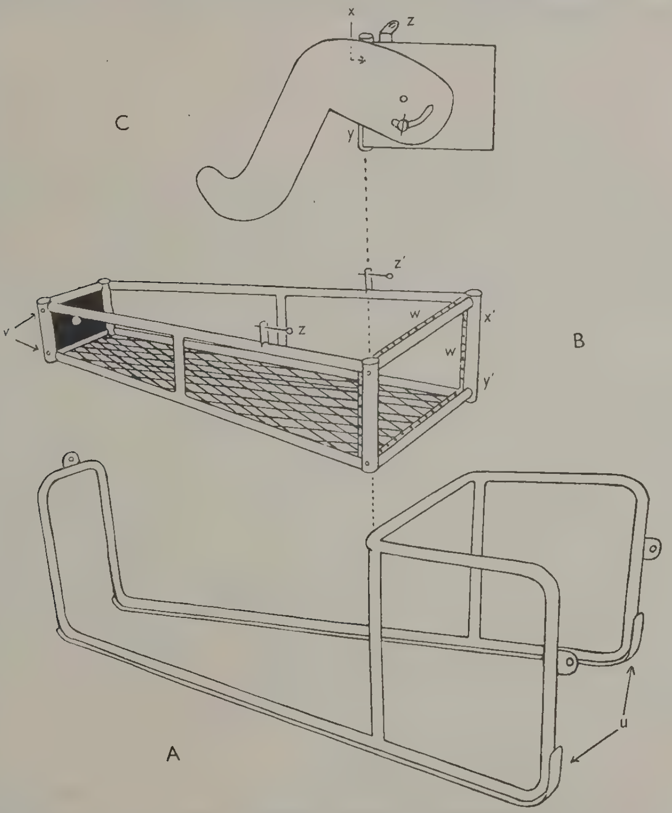

Fig. 3. Portions of the apparatus: A, the sledge frame; B, the net frame; C, one of the doors complete with arm. *u*, the runners; *v*, threaded holes for wing nuts for clamping net frame on sledge frame, also present at the front end; *w*, steel laths with holes 3 in. apart for hooks of net; *x*, *x'*, *y*, *y'*, position of hinges on door and net frame; *z*, *z'*, points of attachment of springs on door and net frame.

duration of tow varied somewhat according to circumstances, but was usually 20 min. to ensure an adequate catch, though this was often much more than sufficient.

The catches obtained were not appreciably contaminated with sand or mud if the apparatus had been working properly, even with the net frame fixed at its lowest possible position on the sledge frame. Small coal particles, extremely abundant in the sea in this area, however, often contaminated the catches and had to be separated off in the laboratory later.

A detailed analysis of the catches will be discussed in a subsequent paper.

## Possible Improvements in Design of the Apparatus

The model employed so far is an experimental one, and a number of improvements have suggested themselves during the course of the work with it. Minor ones include, amongst others, better streamlining of the frame, perhaps a greater range of vertical movement of the net frame on the sledge frame, and the attachment of the bucket to the net by means of a bayonet clip. Total weight cannot be much reduced in future models, especially if the apparatus is to be used in any appreciable depth of water, unless a paravane system is mounted which will carry it to and keep it at the bottom without disturbing the flow of water into and through the net. Such paravanes would have to be mounted beyond the range of the current system through the net.

The door system should be improved by eliminating the arms which project out at right angles and render the apparatus rather more clumsy than is necessary, and placing others *beneath* the frame. In addition, it is possible that the doors may tend to flap whilst the apparatus is being towed and thus influence the water flow into the net and thereby the catch obtained. The doors could therefore be substituted by a vertically moving, flexible shutter operated by such arms acting against the pull of springs.

However, during visual observation of the present apparatus at work in very shallow water, no flapping of the doors was observed and the motion along the bottom was quite satisfactory.

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# THE SEASONAL ABUNDANCE OF YOUNG FISH
## XI. THE YEAR 1949

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Zoologist at the Plymouth Laboratory

(Text-figs. 1, 2)

The 1949 production of young fish and plankton in Plymouth off-shore waters continued to remain at the low level characteristic of the last few years. Collections were made by half-hour oblique hauls of the 2 m. stramin ring-trawl; the dates are given in Table I. The fortnightly averages of all young fish, excluding clupeids, are shown in Table II with comparative figures for 1948 and for the period 1930–34. The highest value, in the second half of June, may have been unduly weighted, since only one collection was made in the fortnight. The monthly total catches of young fish are given in Table III. The sum of the monthly averages for all young fish (459) was slightly higher than the 1948 value (311[1]), due to larger catches of clupeids; young fish other than clupeids continued to decrease. A few post-larval herring were present in January, and for the third successive year young *Mugil* spp. occurred; two in October and one in December. No young plaice were caught, although a very small number of plaice eggs were present in January and February. Plankton, other than young fish, was very sparse throughout the year, *Calanus* being even scarcer than in 1948. *Sagitta setosa* was the dominant *Sagitta* species, although never abundant, and as in recent years the numbers were particularly low from February to June. A few *S. elegans* occurred in November and December (maximum, 66 specimens). The abundance and percentages of the *Sagitta* species are shown in Fig. 1.

In the account of conditions in 1948, it was noted that small immature *S. setosa* appeared to predominate in the catches, indicating perhaps a further step in the progressive decline of the macroplankton of the area. In order to examine this question, the maturity stages of all the 1949 catches of *setosa* were determined. But the low numbers caught preclude any reliable information concerning trends in the proportions of the stages, and make it difficult to interpret the data regarding the numbers of mature populations and of spawnings during the year. It would seem, however, that there were not more than five mature populations and probably only five spawnings. This, in contrast to at least six breeding populations and eight spawnings in the period September 1930—August 1931 (Russell, 1932), points to a considerably lowered productivity.

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[1] Misprinted as 331 in the 1948 report.

Three specimens of *Muggiaea atlantica*, which was present throughout 1948, occurred in January and February. During the summer no *Muggiaea* were caught, until small numbers of *M. kochi* appeared in October–December (maximum, 33 specimens). Three small *Aglantha* were present in the catch of 14 November. *Liriope*, which occured in considerable quantity at the end of 1948, continued to be present in 1949 until 1 February. A single salp was taken on 5 January and one *Themisto* on 20 January.

The numbers of pilchard eggs in the catches are given in Table IV. The monthly averages have again fallen very considerably since the low averages of 1948.

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1949

All 2 miles east of Eddystone, unless otherwise stated

| Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 1* | 7 | 11 | 2† | 8 | 1 | 3 | 1 | 4 | 7 | 8 |
| 5* | 7 | 14 | 13* | 4 | 9* | 11 | 8* | 5 | 6* | 8* | 12 |
| 10 | 14 | 21 | 14 | 9* | 14 | 22 | 8 | 8* | 8 | 14 | 19 |
| 14‡ | 21 | 29 | 25 | 10 | 24 | 26 | 26 | 12 | 10 | 28 | 22* |
| 14§ | 28 | | 27‡N | 16 | | | | 19 | 17 | | 28 |
| 14 | | | 29N | 24 | | | | 26 | 27 | | |
| 17 | | | 29N | 30 | | | | | | | |
| 20 | | | | | | | | | | | |
| 24 | | | | | | | | | | | |
| 31 | | | | | | | | | | | |

* Station E1. † Station L5. N, night collection.
‡ Station L4. § Station L6.

TABLE II. FORTNIGHTLY AVERAGE CATCHES OF ALL YOUNG FISH EXCLUDING CLUPEIDS, 1930–34, 1948 AND 1949

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1930–34 (average): | | | | | | | | | | | | |
| 1st fortnight | 5 | 10 | 27 | 110 | 635 | 299 | 100 | 152 | 48 | 11 | 7 | 2 |
| 2nd fortnight | 8 | 15 | 89 | 374 | 573 | 78 | 85 | 48 | 9 | 6 | 3 | 2 |
| 1948: | | | | | | | | | | | | |
| 1st fortnight | + | 3 | 15 | 12 | nr | 13 | 9 | 9 | + | 4 | 0 | 1 |
| 2nd fortnight | 0 | 16 | 15 | nr | 65 | 32 | 17 | 5 | 0 | + | + | 0 |
| 1949: | | | | | | | | | | | | |
| 1st fortnight | + | 1 | 0 | 1 | 10 | 22 | 20 | 22 | + | + | 1 | 2 |
| 2nd fortnight | + | + | 2 | 11 | 18 | 77 | 26 | 1 | 1 | 0 | 1 | + |

nr, no records. + average of less than 1.

It is necessary that a note should be included in these records concerning the quality of the stramin used in the 2 m. ring-trawl. Pre-war stramin has an average of sixteen threads in both warp and weft to the inch when dry and unused. It is evenly woven and there is only slight variation in the thickness of the threads, so that the actual holes between the meshes have a very fair uniformity of size; the threads are also free of projecting tufts. Stramin of this quality became unobtainable after the war. The post-war stramin has an average of fourteen threads in the warp and thirteen in the weft to the inch. It is very unevenly woven, the thickness of the strands is extremely variable and

## TABLE III. MONTHLY TOTAL CATCHES OF POST-LARVAE IN HALF-HOUR OBLIQUE HAULS WITH 2 M. STRAMIN RING-TRAWL, 1949

The number of hauls per month is shown by the small figure against each month at the head of the column.
A + is used in the 2nd, 4th and 6th lines to denote monthly average of less than 0·5.

| | Jan.$^{10}$ | Feb.$^{5}$ | Mar.$^{4}$ | Apr.$^{7}$ | May$^{7}$ | June$^{4}$ | July$^{4}$ | Aug.$^{4}$ | Sept.$^{6}$ | Oct.$^{6}$ | Nov.$^{4}$ | Dec.$^{5}$ | Total | Sum of monthly averages |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total young fish | 85 | 11 | 3 | 69 | 314 | 304 | 692 | 272 | 27 | 119 | 189 | 15 | 2100 | .. |
| Monthly average, T.Y.F. | 9 | 2 | 1 | 10 | 45 | 76 | 173 | 68 | 5 | 20 | 47 | 13 | .. | 459 |
| T.Y.F., less clupeids | 5 | 5 | 1 | 49 | 93 | 144 | 94 | 66 | 4 | 3 | 4 | 5 | 473 | .. |
| Monthly average, ditto | 1 | 1 | + | 7 | 13 | 36 | 24 | 17 | 1 | 1 | 1 | 1 | .. | 103 |
| All clupeid spp. | 80 | 6 | 2 | 20 | 221 | 160 | 598 | 206 | 23 | 116 | 185 | 10 | 1627 | .. |
| Monthly average, ditto | 8 | 1 | 1 | 3 | 32 | 40 | 149 | 51 | 4 | 19 | 46 | 2 | .. | 356 |
| *Clupea harengus* | 31 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 31 | 3·1 |
| *Gadus pollachius* | .. | .. | .. | .. | 6 | 1 | .. | .. | .. | .. | .. | .. | 7 | 1·11 |
| *Gadus merlangus* | .. | .. | .. | .. | 3 | 5 | .. | .. | .. | .. | .. | .. | 8 | 1·68 |
| *Gadus minutus* | .. | .. | .. | 7 | .. | .. | .. | .. | 11 | .. | .. | .. | 7 | 1·0 |
| *Gadus luscus* | 3 | 2 | .. | .. | .. | .. | .. | .. | .. | .. | 2 | 3 | 10 | 1·8 |
| *Gadus callarias* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Onos* spp. | .. | .. | .. | 3 | 26 | 11 | 3 | .. | .. | .. | .. | .. | 43 | 7·88 |
| *Phycis blennoides* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Molva molva* | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. | 1 | 0·14 |
| *Merluccius merluccius* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Raniceps raninus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Capros aper* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Zeus faber* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Arnoglossus* spp. | .. | .. | .. | .. | .. | 1 | 8 | 9 | 1 | .. | .. | .. | 19 | 4·67 |
| *Rhombus* spp. | .. | .. | .. | .. | 3 | 2 | .. | .. | 1 | .. | .. | .. | 6 | 1·1 |
| *Scopthalmus norvegicus* | .. | .. | .. | 3 | 1 | | .. | .. | .. | .. | .. | .. | 4 | 0·57 |
| *Zeugopterus punctatus* | .. | .. | .. | 2 | 2 | } 1 { | .. | .. | .. | .. | .. | .. | 4 } 9 | 0·57 } 1·39 |
| *Zeugopterus unimaculatus* | .. | .. | .. | .. | .. | | .. | .. | .. | .. | .. | .. | .. | .. |
| *Pleuronectes platessa* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Pleuronectes limanda* | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 0·14 |
| *Pleuronectes flesus* | .. | .. | .. | .. | 4 | .. | .. | .. | .. | .. | .. | .. | 4 | 0·6 |
| *Pleuronectes microcephalus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Solea vulgaris* | .. | .. | .. | .. | 1 | 10 | .. | .. | .. | .. | .. | .. | 11 | 2·64 |
| *Solea variegata* | .. | .. | .. | 2 | 1 | 14 | .. | .. | .. | .. | .. | .. | 17 | 3·94 |
| *Solea lascaris* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Solea lutea* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Serannus cabrilla* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Caranx trachurus* | .. | .. | .. | .. | .. | .. | 8 | 20 | .. | 1 | .. | .. | 29 | 7·17 |
| *Mullus surmuletus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Morone labrax* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Ammodytes lanceolatus* | .. | .. | .. | 4 | 20 | .. | 1 | .. | .. | .. | .. | .. | 25 | 3·85 |
| *Ammodytes tobianus* | .. | .. | .. | | .. | .. | 1 | .. | .. | .. | .. | .. | 1 | 0·25 |
| *Ammodytes marinus* | .. | .. | .. | } 1 { | .. | .. | .. | .. | .. | .. | .. | .. | .. } 8 | .. } 1·49 |
| *Ammodytes immaculatus* | 2 | 2 | 1 | | .. | .. | .. | .. | .. | .. | 1 | .. | 6 | 1·1 |
| *Cepola rubescens* | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. | .. | .. | 2 | 0·39 |
| *Callionymus* spp. | .. | .. | .. | 2 | 13 | 51 | 6 | 10 | .. | .. | .. | .. | 82 | 19·3 |
| *Labrus bergylta* | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | 1 | 0·25 |
| *Labrus mixtus* | .. | .. | .. | .. | 1 | 1 | .. | .. | .. | .. | .. | .. | 2 | 0·39 |
| *Ctenolabrus rupestris* | .. | .. | .. | .. | 5 | 19 | 18 | 2 | .. | .. | .. | .. | 44 | 10·71 |
| *Crenilabrus exoletus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Trachinus vipera* | .. | .. | .. | .. | .. | .. | 3 | 2 | .. | .. | .. | .. | 5 | 1·25 |
| *Scomber scombrus* | .. | .. | .. | .. | .. | .. | 16 | 9 | .. | .. | .. | .. | 25 | 6·25 |
| *Gobius* spp. | .. | .. | .. | 19 | .. | .. | 6 | 4 | .. | .. | 1 | .. | 30 | 5·46 |
| *Lebetus scorpioides* | .. | .. | .. | 1 | 1 | .. | 2 | 1 | .. | .. | .. | .. | 5 | 1·03 |
| *Blennius ocellaris* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Blennius pholis* | .. | .. | .. | 1 | 3 | 3 | .. | .. | .. | .. | .. | .. | 7 | 1·32 |
| *Blennius gattorugine* | .. | .. | .. | .. | 1 | 23 | 21 | 5 | .. | .. | .. | .. | 50 | 12·64 |
| *Chirolophis galerita* | .. | 1 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 0·2 |
| *Mugil* spp. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .. | 1 | 3 | 0·53 |
| *Agonus cataphractus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Trigla* spp. | .. | .. | .. | .. | .. | 1 | 2 | 2 | .. | .. | .. | .. | 5 | 1·25 |
| *Cottus* spp. | .. | .. | .. | 1 | 1 | .. | .. | .. | .. | .. | .. | .. | 2 | 0·28 |
| *Cyclopterus lumpus* | .. | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | 1 | 0·34 |
| *Liparis montagui* | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 0·14 |
| *Lepadogaster bimaculatus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Lophius piscatorius* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Pipe fish | .. | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | 1 | 0·17 |
| Unidentified | .. | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | 1 | 0·17 |

there are noticeably more thinner threads than in the pre-war material. In consequence the mesh holes are considerably larger and very much less uniform than in the pre-war stramin. The threads are also very tufted and fuzzy.

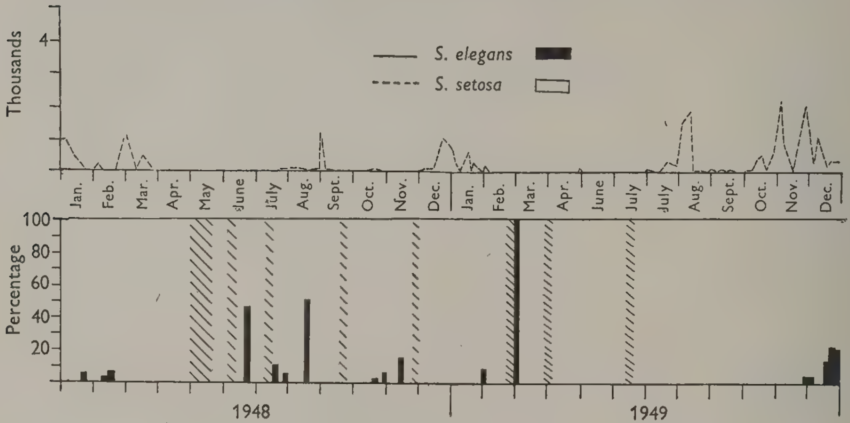

Fig. 1. Above, curves showing the abundance of *Sagitta elegans* (——) and *S. setosa* (-----) in half-hour oblique hauls with the 2 m. stramin ring-trawl in 1948 and 1949. Below, percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched. (Continued from Corbin, 1949, p. 710, fig. 1.)

TABLE IV. PILCHARD EGG CATCHES, 1949

See Table I for dates of hauls

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0* | 0 | 0* | 6 | 630 | 420 | 13 | 0 | 42 | 107 | 0 | 4 |
| | | 3 | | 36 | 590 | 716 | 6 | 0 | 20 | 448 | 0 | 3 |
| | | 63 | | 49 | 412 | 1,610 | 9 | 0 | 96 | 1 | 1 | 1 |
| | | 0 | | 56 | 184 | 568 | 1 | 24 | 2 | 61 | 40 | 0 |
| | | 0 | | 31 | 1,328 | | | | 9 | 1 | | 18 |
| | | | | 157 | 1,160 | | | | 0 | 0 | | |
| | | | | 228 | 836 | | | | | | | |
| Monthly average, 1949 | 0 | 13 | 0 | 80 | 734 | 828 | + | + | 28 | 103 | 10 | + |
| Monthly average, 1937–39 and 1946–47 | + | 0 | + | 478 | 5,868 | 14,093 | 6,196 | 385 | 415 | 305 | 398 | + |

+ Average of less than 10.
* None taken in any haul in these months.

Since it was important that this series of observations should continue, the 2 m. ring-trawls had to be made up in the inferior material despite the discrepancy of mesh size. The post-war stramin has been in use since mid-September 1947.

The larger mesh of the post-war stramin will undoubtedly have resulted in a loss of some of the catch, particularly the smaller organisms. There has certainly been a very marked poverty of copepods in the catches of the last 2 years. On the other hand, considerable numbers of small *Sagitta* and clupeid larvae have at times been caught, and it is possible that the fuzziness of the threads may have had a slight effect in reducing the actual mesh size.

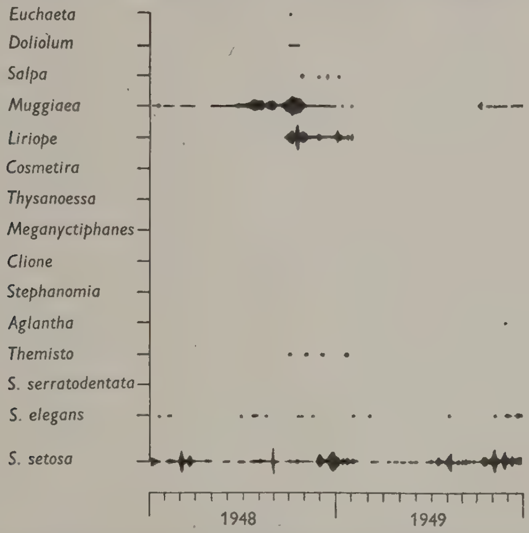

Fig. 2. Diagram showing the occurrence of plankton indicators in the collections off Plymouth in 1948 and 1949. *Note.* The *Muggiaea* present in October–December 1949 were all *M. kochi*. (Continued from Corbin, 1949, p. 711, fig. 2.)

A measure of the loss of catch will be possible by comparative hauls, when stramin of the pre-war quality becomes available.

There is thus some doubt as to the reliability of comparisons between data obtained with the pre- and post-war stramin. Nevertheless, it would seem improbable that major fluctuations would have been obscured, and this appears to be upheld by the continued decline in the sum of the monthly averages of young fish excluding clupeids and in the monthly average catches of pilchard eggs in 1948 and 1949, during both of which years the poorer stramin was in use.

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# NOTE ON A METHOD FOR DETERMINATION OF AMMONIA IN SEA WATER

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Since the estimation of ammonia in sea water by existing methods either presents difficulties or requires much time, an alternative based on a different principle has been explored.

This method depends upon the action of ammonia on sodium hypobromite in an alkaline medium, when

$$2NH_3 + 3NaBrO = N_2 + 3NaBr + 3H_2O.$$

If the sea water is acidified before the hypobromite is added, the ammonia present will not react. The effect therefore may be measured of adding the hypobromite, in equal quantities, to two samples of sea water, one untreated and one acidified. The difference represents an equivalent of ammonia. Excess hypobromite is estimated colorimetrically by adding Bordeaux B dye solution, which is decolorized by the hypobromite in acid solution.

I have the pleasure to thank very gratefully Dr H. W. Harvey, F.R.S., to whom I am much indebted for suggesting the problem, for his criticism and contribution to the work. The discussions with Dr L. H. N. Cooper and Mr F. A. J. Armstrong were also very helpful and I thank them cordially.

This work was done at the Plymouth Laboratory, and I am deeply indebted to the Director, Mr F. S. Russell, F.R.S., for his kindness in allowing me unrestricted facilities in the Laboratory.

## THE METHOD

### *Solutions Required*

(i) Hydrobromic acid 0·23N, containing 1·9 % HBr. (ii) Sodium hypobromite 0·001N, made by diluting 0·1N stock solution, which is prepared by dissolving 2·5 g. NaOH and 1·25 ml. fluid bromine in 500 ml. of distilled water. This 0·001N-NaBrO is made alkaline by adding 1 % of 2N-$Na_2CO_3$. (iii) Bordeaux B, 0·014 g. of dye per litre. (iv) Ammonium sulphate: stock solution; 0·4716 g. $(NH_4)_2SO_4$ per litre; working solution is obtained by diluting 4 ml. of stock solution to 500 ml. 0·25 ml. of this solution contains 2 $\mu$g. ammonia-N.

*Procedure*

Exactly 50 ml. of the sea-water sample is transferred to each of three 100–150 ml. flasks by pipette. Using an all-glass syringe (Krogh's pipette) there is then added to

flask A: 1 ml. of (i) solution, followed immediately by
2 ml. of (ii) solution, followed immediately by
5 ml. of (iii);

flask B: 2 ml. of (ii) and then after 1 min.
1 ml. of (i) followed immediately by
5 ml. of (iii);

flask C: 0·25 ml. of (iv) (which is equivalent to the
addition of 40 mg. ammonia-N/m.$^3$) and
thereafter as for flask B.

The flasks are allowed to stand covered for 2 hr. or more (overnight) and the absorption of blue green light is then measured. Colorimetric measurements are conveniently made in a 4 cm. cuvette in the instrument described by Harvey (1948), the light passing through two Ilford filters, no. 404R + no. 403R.

If $\alpha$, $\beta$ and $\gamma$ is the increase in optical density over that of distilled water, of the contents of the three flasks in the same cuvette, then $\beta - \alpha = K \times$ hypobromite destroyed by ammonia present in the water sample, and $\gamma - \beta = K \times$ hypobromite destroyed by the added 40 mg. ammonium-N/m.$^3$.

The concentration of ammonia in the sample of sea water is therefore $\dfrac{40(\beta-\alpha)}{\gamma-\beta}$ mg. ammonia-N/m.$^3$.

*Example*

The following shows a typical analysis carried out in triplicate on a sample of sea water collected from offshore:

*Difference in Optical Density in 4 cm. Cuvette, Compared with Distilled Water*

| Exp. | $\alpha$ | $\beta$ | $\gamma$ | $\frac{40(\beta-\alpha)}{\gamma-\beta}$ of mg. ammonia-N/m.$^3$ |
|---|---|---|---|---|
| I | 0·305 | 0·338 | 0·381 | 30·7 |
| II | 0·302 | 0·335 | 0·376 | 32·2 |
| III | 0·298 | 0·332 | 0·380 | 28·3 |
| IV | 0·306 | 0·339 | 0·374 | 37·7 |

The values of $\alpha$ in this experiment indicated that 64 % of the added dye had been decolorized.

The $\alpha$ value varies with the concentration of hypobromite solution, which decreases with age; it also varies with different sea-water samples, being greater for harbour waters.

The value of $\gamma - \beta$ bears a strict linear relation to the quantity of ammonia nitrogen added up to a total of about 140 mg. N-NH$_3$/m.$^3$ present. The estimated value of ammonia nitrogen is not affected by the addition of 10 mg./l. of glucose and is not significantly affected by the addition of 40 mg. nitrite nitrogen per m.$^3$. When amino-acetic acid is added, about 30 % of the amino-nitrogen behaves as ammonia. During storage the ammonia content of unfiltered sea waters was found to decrease, as had been observed by Redfield & Keys (1938).

### *Comparison with Determinations Made by Distilling Sea Water in a Current of Air under Reduced Pressure*

The method of Krogh (1934) was followed, 30 ml. of sea water (at pH 10–11 obtained by adding 0·25 N-NaOH, using cresol phthalein as indicator) being distilled in a current of air at a pressure of 70–80 mm. mercury.

The use of a 0·006 % solution of potassium indigo disulphonate, instead of napthyl red, gave a sharper end-point and obviated the necessity of titrating each sample at the same speed and of thoroughly cleaning the titration vessels in order to rid them of all traces of oxidation products of napthyl red. Traces of these products interfere with the titration (Buljan, 1951).

It was found that if amino-acetic acid was added to the sea water, 16–20 % of the amino-nitrogen distilled over as ammonia. Hence in both methods, the estimated values for ammonia nitrogen include a part of any amino-nitrogen present. Determinations carried out by the distillation method, in duplicate from the same sample of unfiltered sea water, did not show close agreement, sometimes differing by as much as 11 mg. ammonia-N/m.$^3$.

The following table gives results (in mg. ammonia-N/m.$^3$) obtained by the two methods:

| | By distillation | By photometric method |
|---|---|---|
| Raw unfiltered sea water collected offshore | 29·9 | 37·7 |
| | 35·6 | 30·7 |
| | 25·3 | 32·2 |
| | 21·8 | 28·3 |
| Mean | 28·15 | 32·2 |
| Another unfiltered sea water collected offshore | 18·1* | 25·5 |
| Stored water | 16·8* | 7·5 |
| Water from Plymouth Sound | 27·8* | 30·8 |
| Polluted sea water (a mixture of water from densely populated aquarium and open sea water) | 40·6* | 48·0 |
| Plymouth Sound sea water with artificially destroyed ammonia | 3·9 | 0·0 |
| Total of means | 135·35 | 144·0 |

* Mean of duplicate determinations.

The totals of the mean values, obtained by each method, are similar. Differences between replicate values appear to be due to similar experimental errors inherent in both methods.

The photometric method is more simple and rapid than distillation.

The time available for this investigation did not allow further study of discrepancies between the two methods.

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# AGE AND GROWTH OF *CALLIONYMUS LYRA* L.

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(Plate I and Text-figs. 1–4)

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The Common Dragonet, *Callionymus lyra* L., is one of the commonest fishes in the Plymouth area, and is widely distributed in European seas. Recent reports indicate that it occurs also off the coast of West Africa (Fowler, 1936; Poll, 1949). This fish, like others of the genus, attracts attention because, although it has very little economic importance, it is strikingly coloured and the sexes are markedly different. Work has been done on the breeding by Holt (1897, 1898), and by Holt & Scott (1898); on ova and larvae by M'Intosh (1885), M'Intosh & Prince (1889), Cunningham (1891), Holt (1897), Ehrenbaum (1905–9), Fage (1918), Mielck (1925), Duncker, Ehrenbaum, Kyle, Mohr & Schnakenbeck (1929); on seasonal abundance and distribution of post-larvae off Plymouth by Russell (1930–47) and Corbin (1948); and on the skeleton by Günther (1861) and Ford (1937). The mature males are provided with remarkable secondary sexual characters both in coloration and in relative lengths of snout and of median fins, which render them so different from the females that they were originally regarded as different species and known as the Gemmeous Dragonet (male *C. lyra* L.) and the Sordid Dragonet (female *C. lyra* L. = *C. dracunculus* L.) respectively (Donovan, 1808; Yarrell, 1859; Couch, 1863). The sexual dimorphism and seasonal variation of this species has been much studied by Holt (1898), Smitt (1892–95), Gallien (1934), Letaconnoux (1949) and Desbrosses (1949). Very little information has so far been provided about its age and growth, with which the present paper deals.

I am greatly indebted to Mr F. S. Russell, F.R.S., for suggesting this investigation to me; and to Mr G. A. Steven for advice and assistance while it was being carried out and for much help in the preparation of the manuscript; to Mr G. M. Spooner for statistical advice and assistance; to Dr T. J. Hart and Mr M. D. Menon for help in the use of the radial bone for age determination; and to Dr J. S. Alexandrowicz who took the photographs. I have also the greatest pleasure in recording my indebtedness to the British Council and to the Trustees of the Ray Lankester fund for financial assistance without which this work could not have been done.

## Collection of the Material

All the specimens for this study were trawled off Plymouth by the research vessels *Sula* and *Sabella* and the research launch *Gammarus* during a period of 18 months, from December 1948 till May 1950. Some young fish were obtained also in the autumn and winter of 1950. During the first few months of the investigation the specimens were caught mainly by ordinary otter-trawl and partly by small beam-trawl (shrimp-netting), and very few fish below 50 mm. in length were collected. In order to obtain more young fish an Agassiz trawl with fine mesh and an otter-trawl with small mesh cover to the cod-end were also used later on. Nevertheless, the difficulty of obtaining sufficient numbers of young fish had not been solved. The total number of fish thus collected for this work amounts to over 4000 specimens varying from 20 to 240 mm. in standard length, including both sexes.

Monthly samples were taken and treated separately. Each fish was labelled and measured to the nearest millimetre, from the tip of the snout to the tip of the distal end of the longest caudal ray (total length) and from the tip of the snout to the distal end of the caudal hypural (standard length or body length). Then they were weighed to the nearest gram in a Salter spring balance and sexed. The large males above 80 mm. can easily be sorted out by means of the male secondary sexual characters, but those below that length were all confirmed by examining the gonads. Before preservation in formalin for other purposes, an otolith or the complete right pectoral girdle, or both of them, were removed and kept in small numbered envelopes for later study.

## Determination of Age and Rate of Growth

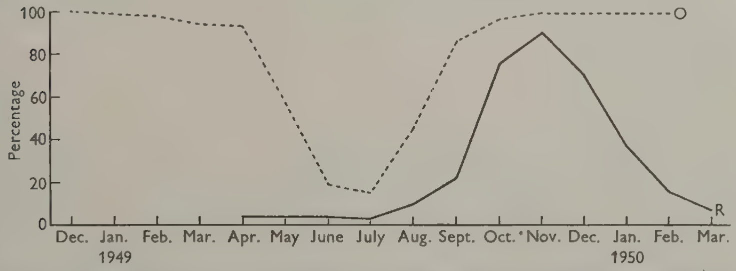
There are no published data on the age and growth of this fish. Dr P. Desbrosses told me, in October 1949, that he had successfully used the otoliths to determine the age of *C. lyra*, but his results have not yet been published.

### *Age Reading from the Otolith*

As *C. lyra* is devoid of scales, the otoliths were at first used for the age determination. The otolith belongs to the labrid type; its outer side is flat, inner side convex, dorsal rim domed and regular, and ventral rim curved (Frost, 1928). It is quite thin, and the number of rings on the fresh otoliths can easily be read under a binocular dissecting microscope against a dark background. If the otolith has been dried it must be immersed in water before examination, otherwise the rings cannot be distinguished easily. The central area of the otolith is opaque, with alternating rings of transparent (slow growth zone) and opaque (rapid growth zone) material. Altogether, 2407 otoliths taken from specimens of various ages of both sexes have been examined, over a period of 15 months, from December 1948 to February 1950 inclusive. The results confirm that the rings on the otoliths are formed annually, as there is a complete turning over of one sort of margin to the other during a certain period of the year (Table I; Text-fig. 1). The opaque rings are laid down cover-

TABLE I. PERCENTAGE OF FISH WITH SLOW OR RAPID GROWTH ZONES AT THE MARGIN OF THE OTOLITH AND OF THE SECOND RADIAL BONE

| | | Percentage of otoliths with | | | Percentage of radial bones with | |
|---|---|---|---|---|---|---|
| Month | No. examined | slow growth zone at the margin | rapid growth zone at the margin | No. examined | slow growth zone at the margin | rapid growth zone at the margin |
| Dec. 1948 | 72 | 100 | 0 | — | — | — |
| Jan. 1949 | 200 | 99 | 1 | — | — | — |
| Feb. 1949 | 119 | 98 | 2 | — | — | — |
| Mar. 1949 | 64 | 94 | 6 | — | — | — |
| Apr. 1949 | 88 | 93 | 7 | 45 | 4 | 96 |
| May 1949 | 101 | 57 | 43 | 126 | 4 | 96 |
| June 1949 | 206 | 19 | 81 | 134 | 4 | 96 |
| July 1949 | 390 | 15 | 85 | 97 | 3 | 97 |
| Aug. 1949 | 230 | 43 | 57 | 162 | 10 | 90 |
| Sept. 1949 | 146 | 86 | 14 | 95 | 22 | 78 |
| Oct. 1949 | 82 | 96 | 4 | 75 | 75 | 25 |
| Nov. 1949 | 124 | 99 | 1 | 274 | 90 | 10 |
| Dec. 1949 | 164 | 99 | 1 | 311 | 70 | 30 |
| Jan. 1950 | 241 | 99 | 1 | 236 | 37 | 63 |
| Feb. 1950 | 180 | 99 | 1 | 177 | 18 | 82 |
| Mar. 1950 | — | — | — | 132 | 7 | 93 |



Text-fig. 1. *Callionymus lyra*, *O* (broken line), percentages of otoliths with transparent (slow growth) zone at margin, from December 1948 till February 1950. *R* (continuous line), percentages of radial bones with slow growth zone at margins, from April 1949 till March 1950.

ing the outer margin of the transparent zone during the summer months. It is a gradual increase in intensity of calcification rather than an increase in width during a short period. The transparent zone begins to appear after July, and the percentage of otoliths with the transparent margin reaches its peak (99–100%) during the winter and early spring. By reading the rings on the otoliths the age and the particular year group to which a fish belongs can be determined without difficulty. Nevertheless, the margins of the rings are very diffuse and the size of the otoliths is subject to great variation. It is very difficult to fix the centre and the line of growth. Although the otolith has been used successfully in reading the age of the fish, it is not practicable to measure it for back-calculation of growth rate. Soon my attention turned towards the other skeletal structures of the fish, since many bones in other fishes have been widely used for age determination (see Menon, 1950).

### *Age and Rate of Growth from the Second Radial Bone*

On the vertebrae, coracoid, hypural and radials of *C. lyra*, there are very obvious alternating transparent and opaque zones, as found also in some bones of other fishes. After careful study, the zones on the second radial were found to be very constant, and the number of zones had a definite relationship with that on the otoliths of the same specimen. This bone was therefore selected for further study.

As a result of the great expansion of the pectoral girdle in *C. lyra*, the second radial bone becomes very flat and greatly enlarged. Its upper and lower surfaces are ossified, and in between the surface layers is the cartilage. During the autumn and winter the margin of the bone becomes almost completely ossified. Thus the narrow, ossified zone (i.e. the slow growth zone or winter ring) is formed.

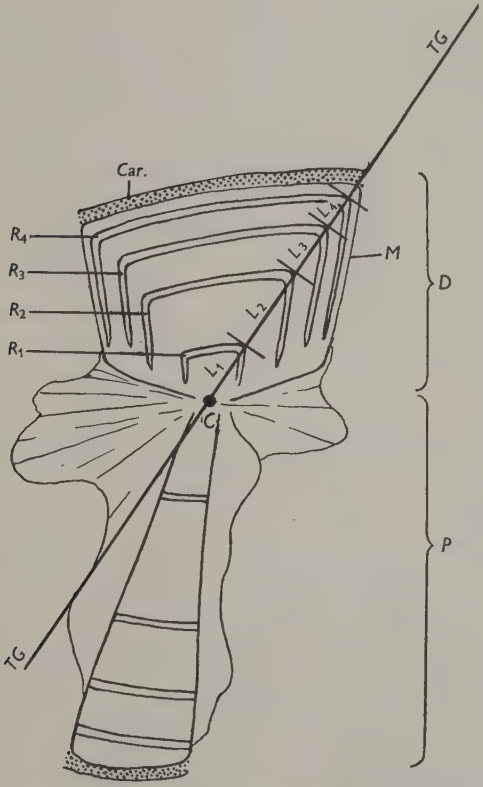
#### *Method of Preparation*

The method of preparing the bone is very easy. After the specimens are measured and numbered, the complete right pectoral girdles are removed one by one with a pair of dissecting scissors, and put into numbered glass dishes. Then they are dipped into a hot bath of water at 70–80° C. for 2-3 min. After this simple treatment, the complete girdle can readily be cleaned with a cloth between the fingers or in a pair of curved forceps. The pectoral girdles of small specimens less than about 80 mm. long are rather delicate, and must be carefully cleaned with forceps under the dissecting microscope, after which they are placed in labelled envelopes and left to dry.

#### *Line of Growth and Method of Measurement*

The distal half of the radial bone grows in three directions, as shown in Text-fig. 2. The centre of growth of the bone is very clear. If a straight line is drawn from the centre towards the angle of the bone, it crosses all the angles of the ossified rings. The measurements taken were along this line, the intervals $L_1$, $L_2$, $L_3$, etc., representing successive annual increments.

Since the radial is a cartilage bone, it shrinks a great deal after drying. The surface is no longer flat and the zones have lost their original shape. Therefore the radial bone of this fish has to be soaked for one to several days before measuring. After this treatment the bone recovers its former size and shape, and the rings become as clear as if the bone were fresh. As the radial bone is not thin enough for projecting, it was measured under a low-power microscope with an eye-piece micrometer.



Text-fig. 2. The second radial bone of *Callionymus lyra* L. Diagram showing the theoretical growth line, and the way of measuring the length of the bone and the annual increments at different ages. *TG*, the hypothetical line of growth; $R_1$ to $R_4$, the annual rings; *C*, the centre of growth; $L_1$, $L_2$, $L_3$ and $L_4$, the first, second, third and fourth years' growth of the second radial bone; *Car.*, cartilage layer; *M*, margin of the bone.

### *Validity of the Zones for Age Determination*

The main evidence supporting the validity of age determination from the second radial in this fish is that the rings on the bone are formed annually.

Monthly observations on the nature of the margins of the second radial were carried out over one complete year. Altogether 1860 radials were examined specially for this test. The results obtained, together with those of the otoliths, are given in Table 1 and Text-fig. 1. The data reveal two important points: (i) that there is a nearly complete turning over in a certain period of the year from one kind of margin to the other, and (ii) that there is also a definite agreement between the number of rings on the radial and that on the otoliths. In the second radial bone the narrow ossified zone (the slow-growth zone or winter ring) begins to appear in September. Its percentage occurrence is highest in November and falls rapidly after December. Usually, in young fish, the formation of the first ring takes place comparatively early, whereas in some of the mature fish the completion of the rings is much delayed. Therefore, there is no complete turning over from one kind of margin to the other throughout the entire population at any period.

From the above evidence there can be no doubt that the zones on the second radial are annual, and it is therefore concluded that the second radial is valid for age determination in this fish.

## RESULTS OF GROWTH MEASUREMENTS

Altogether 1059 second radials from male fish and 627 from females were measured. Among the 1059 male radials 876 were from immature and 183 from mature fish.

The mean lengths of both body and radial at each 5 mm. group in the immature males and females are given in Table II. When the mean radial lengths are plotted against the mean body lengths all the points lie practically along a straight line, as shown in Text-fig. 3.

The snout in mature males is greatly prolonged and subjected to great variation. As its length is correlated with the state of sexual maturity and is not in direct proportion to the body length, correction must be made in total length measurements for the excess of snout length (see p. 289). After this correction has been made and the mature males regrouped, the proportion of the mean lengths of the radials and the corrected body length in different length groups came into agreement with those of the immature males and the females (Table VI; Text-fig. 3).

By graphic method the formula for the correlation curve of the radial length and the body length in this fish is as follows

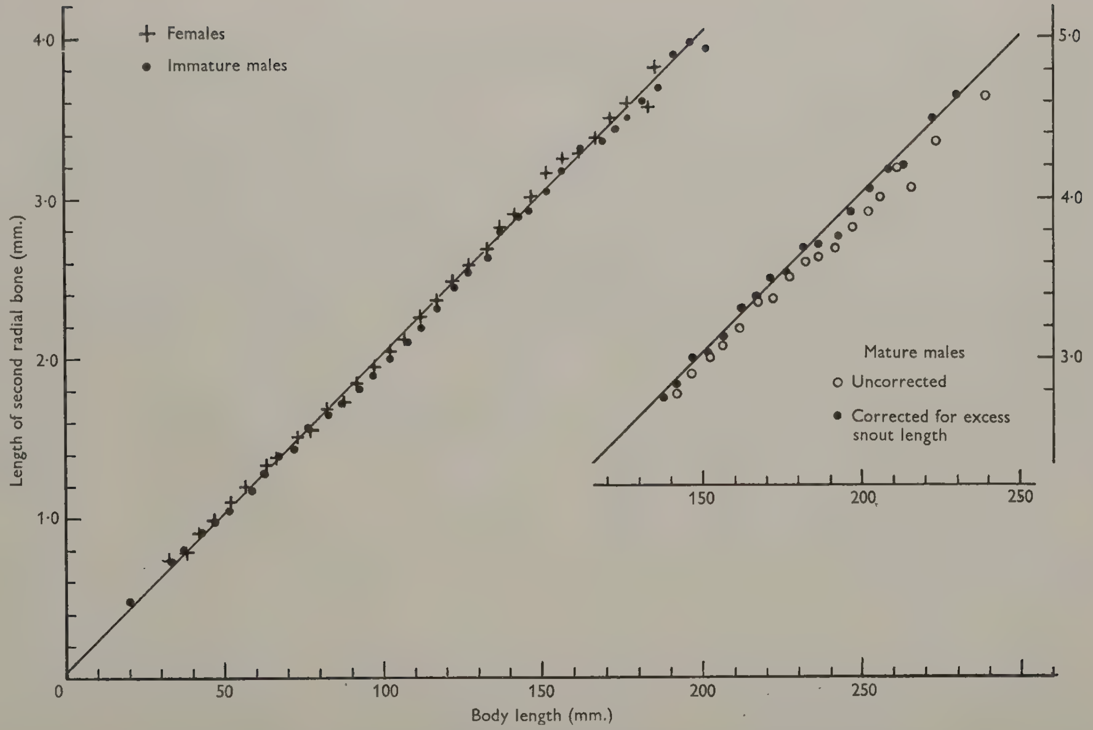
$$R = 0{\cdot}04 + 0{\cdot}0199\,B,$$

where $R$ is the length of the radial and $B$ is the body length; both measured in mm. By using this formula the theoretical lengths of either radial bone or the body length of each 5 mm. group above 35 mm. can be worked out, given one or the other. In Table II the calculated body lengths (given the observed radial bone lengths) are listed for immature males and females, and in Table VI for mature males. The differences between the empirical lengths and the calculated lengths of the body are less than 5 mm. except at a few points.

TABLE II. MEAN LENGTHS OF THE SECOND RADIAL IN RELATION TO THE MEAN LENGTH OF FISH AT THE DIFFERENT LENGTH GROUPS

| | Immature males | | | | | Females | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Length group (mm.) | No. of fish | Mean body length (mm.) | Length of 2nd radial (mm.) | | Theoretical body length (mm.) | No. of fish | Mean body length (mm.) | Length of 2nd radial (mm.) | | Theoretical body length (mm.) |
| | | | mean | σ | | | | mean | σ | |
| 20 | 1 | 20·0 | 0·48 | — | 22·1 | 0 | — | | — | — |
| 25 | 0 | — | — | — | — | 0 | | — | — | — |
| 30 | 4 | 33·2 | 0·73 | 0·03 | 34·7 | 4 | 32·8 | 0·74 | 0·02 | 35·2 |
| 35 | 5 | 37·2 | 0·80 | 0·06 | 38·2 | 12 | 36·8 | 0·79 | 0·07 | 37·7 |
| 40 | 15 | 42·8 | 0·91 | 0·05 | 43·7 | 19 | 42·1 | 0·91 | 0·05 | 43·7 |
| 45 | 11 | 47·1 | 0·98 | 0·02 | 47·2 | 9 | 46·8 | 0·99 | 0·05 | 47·7 |
| 50 | 7 | 57·4 | 1·04 | 0·05 | 50·3 | 6 | 52·0 | 1·10 | 0·05 | 53·3 |
| 55 | 7 | 58·6 | 1·17 | 0·07 | 56·8 | 6 | 56·7 | 1·20 | 0·05 | 58·3 |
| 60 | 4 | 62·7 | 1·28 | 0·08 | 62·3 | 7 | 63·1 | 1·33 | 0·04 | 64·8 |
| 65 | 6 | 67·2 | 1·39 | 0·06 | 67·8 | 10 | 66·6 | 1·38 | 0·06 | 67·3 |
| 70 | 7 | 72·0 | 1·43 | 0·05 | 69·8 | 6 | 73·0 | 1·51 | 0·11 | 73·9 |
| 75 | 9 | 76·7 | 1·56 | 0·07 | 76·4 | 17 | 76·6 | 1·56 | 0·10 | 76·4 |
| 80 | 9 | 82·6 | 1·65 | 0·07 | 80·9 | 14 | 82·0 | 1·68 | 0·08 | 82·4 |
| 85 | 15 | 87·0 | 1·72 | 0·06 | 84·4 | 24 | 87·2 | 1·73 | 0·07 | 84·9 |
| 90 | 32 | 92·4 | 1·81 | 0·09 | 88·9 | 46 | 91·8 | 1·84 | 0·08 | 90·5 |
| 95 | 43 | 97·0 | 1·89 | 0·07 | 93·0 | 46 | 97·2 | 1·95 | 0·09 | 96·0 |
| 100 | 45 | 102·0 | 2·00 | 0·08 | 98·5 | 40 | 102·0 | 2·04 | 0·09 | 100·5 |
| 105 | 55 | 107·4 | 2·10 | 0·08 | 103·5 | 43 | 106·8 | 2·12 | 0·09 | 104·5 |
| 110 | 50 | 111·9 | 2·19 | 0·10 | 108·0 | 32 | 111·9 | 2·26 | 0·10 | 111·6 |
| 115 | 43 | 117·0 | 2·31 | 0·08 | 114·1 | 35 | 117·0 | 2·36 | 0·11 | 116·6 |
| 120 | 37 | 122·1 | 2·44 | 0·10 | 120·6 | 44 | 121·8 | 2·48 | 0·10 | 122·6 |
| 125 | 25 | 127·0 | 2·54 | 0·10 | 125·6 | 38 | 127·0 | 2·58 | 0·11 | 127·6 |
| 130 | 40 | 131·6 | 2·62 | 0·11 | 129·6 | 20 | 132·3 | 2·68 | 0·09 | 132·7 |
| 135 | 30 | 137·1 | 2·79 | 0·12 | 138·2 | 29 | 136·6 | 2·81 | 0·11 | 139·2 |
| 140 | 23 | 142·9 | 2·88 | 0·09 | 142·7 | 25 | 141·6 | 2·90 | 0·14 | 143·7 |
| 145 | 36 | 146·8 | 2·92 | 0·13 | 144·7 | 21 | 146·8 | 3·01 | 0·18 | 149·2 |
| 150 | 35 | 151·7 | 3·04 | 0·13 | 150·8 | 18 | 151·5 | 3·16 | 0·11 | 156·8 |
| 155 | 30 | 156·3 | 3·17 | 0·10 | 157·3 | 13 | 156·7 | 3·25 | 0·13 | 161·3 |
| 160 | 36 | 162·0 | 3·31 | 0·14 | 164·3 | 19 | 161·5 | 3·29 | 0·14 | 163·3 |
| 165 | 42 | 166·9 | 3·36 | 0·15 | 166·8 | 7 | 167·0 | 3·38 | 0·10 | 167·8 |
| 170 | 49 | 172·6 | 3·43 | 0·14 | 170·4 | 10 | 171·1 | 3·50 | 0·18 | 173·9 |
| 175 | 39 | 176·4 | 3·50 | 0·13 | 173·9 | 2 | 176·5 | 3·59 | 0·24 | 178·4 |
| 180 | 37 | 181·5 | 3·60 | 0·13 | 178·9 | 3 | 183·0 | 3·57 | 0·08 | 177·4 |
| 185 | 25 | 186·4 | 3·68 | 0·15 | 182·9 | 2 | 185·0 | 3·81 | 0·04 | 189·4 |
| 190 | 12 | 191·6 | 3·89 | 0·16 | 193·5 | — | — | — | — | — |
| 195 | 4 | 196·5 | 3·97 | 0·19 | 197·5 | — | — | — | — | — |
| 200 | 7 | 201·2 | 3·92 | 0·16 | 195·0 | — | — | — | — | — |

An analysis of the length frequency in relation to the number of rings on the 2nd radial bone shows that the male may attain an age of 5 years (with four complete ossified winter rings), while the females may live 2 years longer



Text-fig. 3. Relation between body length and length of the second radial bone.

The graph line in the inset is identical with that in the main diagram, showing that the 'corrected' males conform with the females and immatures.

(with six complete ossified winter rings). However, the males grow much more quickly and to a larger size than the females (Table III).

It is also shown that among the 1059 radials from male fish, 1024 have one or more ossified winter rings; 680 radials have two or more; 164 radials have three or more; and only six radials have four complete ossified winter rings. If the mean lengths of the 1st, 2nd, 3rd and 4th rings are worked by back-calculation derived from the radial, the annual increment of the body length can be obtained irrespective of the actual length of the fish. Similarly, the annual increment of the body length in females at different ages can be calculated (Tables IV and V; Text-fig. 4).

The mean lengths of both the body and the radial of the mature males are entered in Table VI. When mean lengths of radials are plotted against the mean fish lengths, nearly all the points are far below the correlation curve for the immature males and the females (Text-fig. 3). If the snout length in the mature males be corrected according to the following averages derived from the immature males, all the points lie very close to the correlation curve of mean radial length and body length of both immature males and females:

$$\text{snout length (mm.)} = -0{\cdot}3625 + 0{\cdot}1275 \times \text{body length.}$$

## NATURAL DEATH OF THE SPENT MALES

During the spring and summer of 1949, some interesting phenomena were observed. First, sexual maturity in the males was not directly related to the length of the body, since the spawning males varied from about 130 mm. to nearly as long as 240 mm., and at the same time many large immature males were found in the catches (Table VII). Secondly, the majority of the spawning males lost weight very quickly after the breeding season started, generally in the latter part of January off Plymouth, and their secondary sexual characters became extremely prominent. Thirdly, the majority of spent males suddenly disappeared after June and July. This sudden disappearance could be explained in three ways: (i) by degeneration or reabsorption of all the secondary sexual characters, (ii) by migration of the spent males to deeper waters after the breeding season, and (iii) by natural death of the spent males after the breeding season. However, there was no evidence to support the first two possibilities.

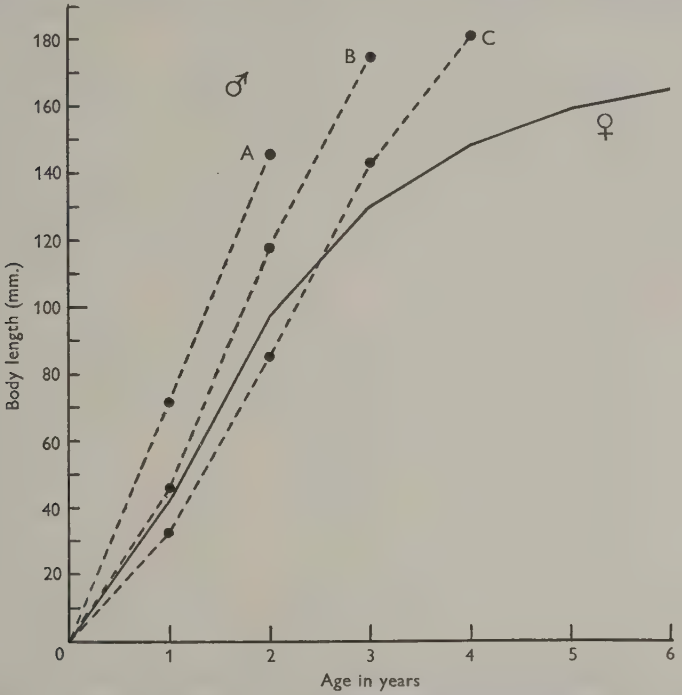
An analysis of the age of all the males collected from April 1949 to March 1950 inclusive, shows that the spawning males clearly fall into three age groups and that all the year round there are mature males; but the percentages of such fish exceeding 120 mm. in length (the size of the smallest mature males) showed a tremendous seasonal change. It was as low as 4·4% in October and as high as 78·1% in March (Table VI). Throughout the 20 months of direct observations on the catches, the gradual changes in the development of the secondary sexual characters in the males could easily be followed, and there was no indication of any recovery of the body condition

# TABLE III. LENGTH FREQUENCIES OF FISH AND RELATION TO NUMBER OF OSSIFIED RINGS ON THE SECOND RADIAL BONES

Mature males enumerated separately in heavy type

| Length group (mm.) | Males. Ossified rings on second radials | | | | | | Females. Ossified rings on second radials | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1+ | 2+ | 3+ | 4+ | Total | 0 | 1+ | 2+ | 3+ | 4+ | 5+ | 6+ | Total |
| 20 | 1 | — | — | — | — | 1 | 0 | — | — | — | — | — | — | — |
| 25 | 0 | — | — | — | — | 0 | 0 | — | — | — | — | — | — | — |
| 30 | 4 | — | — | — | — | 4 | 3 | 1 | — | — | — | — | — | 4 |
| 35 | 5 | — | — | — | — | 5 | 4 | 8 | — | — | — | — | — | 12 |
| 40 | 11 | 4 | — | — | — | 15 | 14 | 5 | — | — | — | — | — | 19 |
| 45 | 7 | 4 | — | — | — | 11 | 5 | 4 | — | — | — | — | — | 9 |
| 50 | 2 | 5 | — | — | — | 7 | 2 | 4 | — | — | — | — | — | 6 |
| 55 | 3 | 5 | — | — | — | 8 | 0 | 6 | — | — | — | — | — | 6 |
| 60 | 1 | 3 | — | — | — | 4 | 0 | 6 | 1 | — | — | — | — | 7 |
| 65 | 1 | 5 | — | — | — | 6 | 1 | 9 | 0 | — | — | — | — | 10 |
| 70 | — | 7 | — | — | — | 7 | 0 | 6 | 0 | — | — | — | — | 6 |
| 75 | — | 7 | 2 | — | — | 9 | 1 | 14 | 2 | — | — | — | — | 17 |
| 80 | — | 7 | 2 | — | — | 9 | — | 8 | 6 | — | — | — | — | 14 |
| 85 | — | 12 | 3 | — | — | 15 | — | 14 | 10 | — | — | — | — | 24 |
| 90 | — | 19 | 13 | — | — | 32 | — | 30 | 16 | — | — | — | — | 46 |
| 95 | — | 37 | 6 | — | — | 43 | — | 26 | 20 | — | — | — | — | 46 |
| 100 | — | 32 | 13 | — | — | 45 | — | 23 | 17 | — | — | — | — | 40 |
| 105 | — | 36 | 19 | — | — | 55 | — | 26 | 17 | — | — | — | — | 43 |
| 110 | — | 36 | 14 | — | — | 50 | — | 17 | 15 | — | — | — | — | 32 |
| 115 | — | 32 | 11 | — | — | 43 | — | 14 | 15 | 6 | — | — | — | 35 |
| 120 | — | 26 | 11 | — | — | 37 | — | 6 | 30 | 8 | — | — | — | 44 |
| 125 | — | 15 | 10 | — | — | 25 | — | 8 | 24 | 6 | — | — | — | 38 |
| 130 | — | 20 | 20 | — | — | 40 | — | 2 | 14 | 3 | 1 | — | — | 20 |
| 135 | — | 10 | 17 | 3 | — | 30 | — | 1 | 18 | 9 | 1 | — | — | 29 |
| 140 | — | 7 + **1** | 15 + **6** | 1 | — | 30 | — | 1 | 10 | 14 | — | — | — | 25 |
| 145 | — | 8 + **1** | 26 + **6** | 2 + **1** | — | 44 | — | 1 | 7 | 12 | 1 | — | — | 21 |
| 150 | — | 2 + **0** | 32 + **8** | 1 + **3** | — | 46 | — | — | 2 | 15 | 1 | — | — | 18 |
| 155 | — | 0 + **0** | 30 + **8** | 0 + **5** | — | 43 | — | — | 4 | 6 | 3 | — | — | 13 |
| 160 | — | 1 + **1** | 30 + **3** | 5 + **6** | — | 46 | — | — | 1 | 11 | 7 | — | — | 19 |
| 165 | — | 1 | 40 + **3** | 1 + **11** | — | 56 | — | — | — | 2 | 5 | — | 1 | 7 |
| 170 | — | — | 41 + **6** | 8 + **9** | — | 64 | — | — | — | 3 | 5 | 1 | — | 10 |
| 175 | — | — | 35 + **8** | 4 + **17** | — | 64 | — | — | — | — | 2 | — | — | 2 |
| 180 | — | — | 31 + **0** | 6 + **7** | **1** | 45 | — | — | — | — | 1 | 2 | — | 3 |
| 185 | — | — | 21 + **1** | 4 + **11** | — | 37 | — | — | — | — | 2 | — | — | 2 |
| 190 | — | — | 10 + **2** | 2 + **10** | — | 24 | — | — | — | — | — | — | — | — |
| 195 | — | — | 2 + **3** | 2 + **10** | — | 17 | — | — | — | — | — | — | — | — |
| 200 | — | — | 7 + **1** | **9** | **2** | 19 | — | — | — | — | — | — | — | — |
| 205 | — | — | — | **7** | **1** | 8 | — | — | — | — | — | — | — | — |
| 210 | — | — | — | **3** | — | 3 | — | — | — | — | — | — | — | — |
| 215 | — | — | — | **5** | **1** | 6 | — | — | — | — | — | — | — | — |
| 220 | — | — | — | **4** | **1** | 5 | — | — | — | — | — | — | — | — |
| 225 | — | — | — | — | — | 0 | — | — | — | — | — | — | — | — |
| 230 | — | — | — | — | — | 0 | — | — | — | — | — | — | — | — |
| 235 | — | — | — | **1** | — | 1 | — | — | — | — | — | — | — | — |
| Totals | 35 | 341 | 461 | 39 | — | 1059 | — | — | — | — | — | — | — | — |
| | | **3** | **55** | **119** | **6** | — | 30 | 240 | 229 | 95 | 29 | 3 | 1 | 627 |

of the spent males or reabsorption of the secondary sexual characters. The most distinct feature of the secondary sexual characters other than coloration is the great prolongation of the snout and of all the median fins, including the dorsal, anal and caudal fins. The prolongation of the snout is mainly effected by the elongation of the process of the premaxillary (Günther, 1861, pp. 140–2). For example, the premaxillary of a spent male, 166 mm. long,



Text-fig. 4. Growth of *Callionymus lyra*. ♂ (broken line), A, third-year breeder; B, fourth-year breeder; C, fifth-year breeder. ♀ (continuous line), mixed.

TABLE IV. MEAN LENGTH OF SUCCESSIVE ANNUAL RINGS

| | Male | | | | Female | | | |
|---|---|---|---|---|---|---|---|---|
| | No. | Range | Mean length (mm.) | S.D. | No. | Range | Mean length (mm.) | S.D. |
| 1st ring | 1024 | 0·39–1·90 | 1·04 | 0·28 | 597 | 0·40–1·90 | 0·88 | 0·27 |
| 2nd ring | 680 | 0·68–2·08 | 1·37 | 0·27 | 357 | 0·58–1·98 | 1·14 | 0·26 |
| 3rd ring | 159 | 0·30–1·88 | 1·10 | 0·31 | 128 | 0·22–1·40 | 0·69 | 0·28 |
| 4th ring | 6 | 0·46–1·04 | 0·81 | 0·23 | 33 | 0·10–0·80 | 0·41 | 0·19 |
| 5th ring | — | — | — | — | 4 | 0·20–0·36 | 0·25 | 0·36 |
| 6th ring | — | — | — | — | 1 | — | 0·16 | 0·00 |

collected in May 1949, reached 28 mm., while an immature one 168 mm. long, collected in the same month, was only 22 mm. long. The length of the first dorsal fin-ray of the former was 125 mm. and of the latter 51 mm. In two other specimens, one a mature male, 204 mm. long (May 1949), and the other an immature male, 201 mm. long (November 1949), the lengths of the premaxillary were 40 and 29 mm., and of the first dorsal fin-rays 145 and 95 mm. respectively. Since the fin-ray and the ossified premaxillary are not epidermal structures, they are very different from the nuptial organ (or pearl organs) found in many fresh-water fishes, which can be dropped off after the breeding season (Kimura & Tao, 1937) and the fleshy hump on the forehead of the cichlids (Cichlidae), which is absorbed after the breeding season (Norman, 1947, p. 301). The possibility of sudden absorption of the skeletal structure or of the greatly elongated fin-rays in this fish would seem impossible.

TABLE V. THEORETICAL LENGTHS CALCULATED FROM MEASUREMENTS OF THE SECOND RADIAL BONES (MM.)

| | Male | | Female | |
|---|---|---|---|---|
| Towards the end of | Annual increment | Cumulative length | Annual increment | Cumulative length |
| 1st ring | 50·3 | 50·3 | 42·2 | 42·2 |
| 2nd ring | 66·8 | 117·1 | 55·3 | 97·5 |
| 3rd ring | 53·3 | 170·4 | 32·7 | 130·2 |
| 4th ring | 38·7 | 209·1 | 18·6 | 148·8 |
| 5th ring | — | — | 10·6 | 159·4 |
| 6th ring | — | — | 6·0 | 165·4 |

No marking experiments have been done to elucidate whether or not the spent males migrate into the deeper water after the breeding season. But the age composition of the mature males in the spring of 1949 is similar to that in the spring of 1950. Here we may take the proportion of the spawning males in the month of April 1949 and those of March 1950 for comparison. The numbers of the third-year, fourth-year and fifth-year breeders in April are 10, 21 and 1; and in March 1950 are 24, 52 and 3 respectively. If the spent males did come back to breed again, the age distribution of the spawning males in the spring of 1950 should have included many more fifth-year breeders. Attempts have been made to study the histological structures of the testis at different stages, and to find out how they are correlated with the secondary sexual characters and seasonal changes, but the data so obtained have not yet been analysed.

Turning to the positive evidence that natural death takes place in the males after the breeding season, the age and rate of growth of 153 spent males were studied in detail. These comprised forty third-year breeders (with two complete winter rings), 107 fourth-year breeders (with three complete winter rings), and six fifth-year breeders (with four complete rings). It was found that the rates of growth of these groups were very different (Table VIII, Text-fig. 4). In those males breeding in the third year the rate of growth was

TABLE VI. *CALLIONYMUS LYRA*, MATURE MALES. LENGTHS OF BODY AND SECOND RADIAL BONE AS OBSERVED, AND AS CORRECTED FOR EXCESS SNOUT LENGTH

| Length group (mm.) | Total specimens | Mean body length (mm.) | Mean length of 2nd radial (mm.) | Ossified rings on second radial (nos. of fish) | | | |
|---|---|---|---|---|---|---|---|
| | | | | 1+ | 2+ | 3+ | 4+ |
| | | | Empirical | | | | |
| 135 | — | — | — | — | — | — | — |
| 140 | 7 | 141·4 | 2·78 | 1 | 6 | — | — |
| 145 | 8 | 146·9 | 2·90 | 1 | 6 | 1 | — |
| 150 | 11 | 152·5 | 3·00 | — | 8 | 3 | — |
| 155 | 13 | 156·5 | 3·07 | | 8 | 5 | — |
| 160 | 10 | 161·4 | 3·19 | 1 | 3 | 6 | — |
| 165 | 14 | 167·1 | 3·35 | — | 3 | 11 | — |
| 170 | 15 | 172·0 | 3·37 | — | 6 | 9 | — |
| 175 | 25 | 177·8 | 3·50 | — | 8 | 17 | — |
| 180 | 8 | 182·4 | 3·60 | — | — | 7 | 1 |
| 185 | 12 | 186·4 | 3·63 | — | 1 | 11 | — |
| 190 | 12 | 191·8 | 3·69 | — | 2 | 10 | — |
| 195 | 13 | 197·2 | 3·81 | — | 3 | 10 | — |
| 200 | 12 | 202·0 | 3·91 | — | 1 | 9 | 2 |
| 205 | 8 | 206·1 | 4·00 | — | — | 7 | 1 |
| 210 | 3 | 210·7 | 4·19 | — | — | 3 | — |
| 215 | 6 | 215·5 | 4·06 | — | — | 5 | 1 |
| 220 | 5 | 223·0 | 4·35 | — | — | 4 | 1 |
| 225 | — | — | — | — | — | — | — |
| 230 | — | — | — | — | — | — | — |
| 235 | 1 | 239·0 | 4·64 | — | — | 1 | — |
| | | | | 3 | 55 | 119 | 6 |
| | | | Corrected | | | | |
| 135 | 3 | 138·0 | 2·75 | 1 | 2 | — | — |
| 140 | 9 | 142·0 | 2·83 | — | 9 | — | — |
| 145 | 7 | 147·4 | 2·99 | 1 | 5 | 1 | — |
| 150 | 15 | 151·9 | 3·03 | — | 8 | 7 | — |
| 155 | 11 | 156·8 | 3·11 | — | 5 | 6 | — |
| 160 | 13 | 161·9 | 3·30 | 1 | 4 | 8 | — |
| 165 | 16 | 167·2 | 3·37 | — | 5 | 11 | — |
| 170 | 9 | 171·2 | 3·49 | — | 3 | 6 | — |
| 175 | 27 | 176·9 | 3·53 | — | 7 | 19 | 1 |
| 180 | 15 | 181·9 | 3·69 | — | 1 | 14 | — |
| 185 | 7 | 186·9 | 3·71 | — | 1 | 6 | — |
| 190 | 19 | 192·4 | 3·76 | — | 3 | 15 | 1 |
| 195 | 8 | 196·6 | 3·91 | — | 1 | 6 | 1 |
| 200 | 15 | 202·6 | 4·05 | — | 1 | 12 | 2 |
| 205 | 3 | 208·2 | 4·17 | — | — | 3 | — |
| 210 | 2 | 213·0 | 4·20 | — | — | 1 | 1 |
| 215 | — | — | — | — | — | — | — |
| 220 | 3 | 220·0 | 4·49 | — | — | 3 | — |
| 225 | — | — | — | — | — | — | — |
| 230 | 1 | 230·0 | 4·64 | — | — | 1 | — |
| 235 | — | — | — | — | — | — | — |
| | | | | 3 | 55 | 119 | 6 |

comparatively very high. Among the forty third-year specimens, the first year's growth of seventeen individuals was higher than the second year's growth, and the mean of the first year's growth is slightly lower than the second year's growth. In those males breeding in the fourth year the rate of twelve specimens was highest in the first year, of eighty highest in the second year, and in only fifteen highest in the third year. The mean of the first year's growth was much smaller than in the other 2 years. Among the males breeding in the fifth year, two specimens showed their highest growth rate in the first year, three in the second year, and one has its third year's growth almost equal to that of the fourth year. As in their growth rates these three groups of breeding males are so different from each other, they must be very different from each other physiologically.

TABLE VII. ACTUAL NUMBERS AND PERCENTAGES OF MATURE MALES ABOVE 120 MM., OBTAINED IN DIFFERENT MONTHS THROUGHOUT ONE COMPLETE YEAR

| Month | No. of mature males | Percentage of mature males |
|---|---|---|
| Apr. 1949 | 42 | 62·7 |
| May 1949 | 90 | 68·7 |
| June 1949 | 55 | 25·3 |
| July 1949 | 34 | 15·0 |
| Aug. 1949 | 10 | 11·8 |
| Sept. 1949 | 11 | 9·8 |
| Oct. 1949 | 4 | 4·4 |
| Nov. 1949 | 16 | 9·2 |
| Dec. 1949 | 64 | 53·3 |
| Jan. 1950 | 28 | 52·8 |
| Feb. 1950 | 39 | 60·9 |
| Mar. 1950 | 89 | 78·1 |
| Total | 482 | — |

TABLE VIII. COMPARISON OF THE RATE OF GROWTH IN THE MALES WHICH BREED AT THE THREE DIFFERENT AGES

| Males breeding in | No. | Successive rings | Lengths of successive rings on radial (mm.) | | Calculated annual increment of body length (mm.) | Calculated mean body length at the end of successive rings (mm.) |
|---|---|---|---|---|---|---|
| | | | mean | $\sigma$ | | |
| 3rd year | 43 | 1st ring | 1·47 | 0·32 | 71·9 | 71·9 |
| | | 2nd ring | 1·50 | 0·27 | 73·4 | 145·3 |
| 4th year | 107 | 1st ring | 0·95 | 0·25 | 45·7 | 45·7 |
| | | 2nd ring | 1·48 | 0·25 | 72·4 | 118·1 |
| | | 3rd ring | 1·16 | 0·28 | 56·3 | 174·4 |
| 5th year | 6 | 1st ring | 0·69 | 0·17 | 32·7 | 32·7 |
| | | 2nd ring | 1·08 | 0·21 | 52·3 | 85·0 |
| | | 3rd ring | 1·19 | 0·25 | 57·8 | 142·8 |
| | | 4th ring | 0·81 | 0·20 | 38·7 | 181·5 |

The presence of large immature males with three complete winter rings on the radial, and of a considerable number of immature males, further proves that the fifth-year male breeders are neither the same third-year breeders of 2 years earlier nor the fourth-year breeders of 1 year earlier. Similarly, the fourth-year breeders are not the third-year breeders of 1 year before.

The length-weight relation and the secondary sexual characters also show that the males of *C. lyra* breed only once in their life. Besides the well-known example of *Anguilla*, which breeds only once during life, *Callionymus lyra* provides one of the most interesting illustrations of natural death among the large fishes.

## SUMMARY

Both the otoliths and the second radials of the pectoral girdle can be used for age determination in *Callionymus lyra* L. Since the latter are far more satisfactory than the former, the second radial was selected for this work and the otolith was used only to check age reading. The radial is here used for the first time for age determination in fish.

The male may live up to 5 years (with four complete ossified winter rings), while the females may live 2 years longer (with six complete ossified winter rings). However, the males grow much quicker and to a larger size (239 mm. long) than the females (185 mm.).

The age of the spawning males falls into three age groups: (A) those that breed in the third year having two complete winter rings; (B) those that breed in the fourth year having three; (C) those that breed in the fifth year having four.

An analysis of the rates of growth of the spent males of three age groups shows that the rate of growth is highest in the third-year breeders, and is lowest in the fifth-year breeders.

Evidence has been given showing that the males of *C. lyra* breed only once and subsequently die. Breeding of the females has not been worked out.

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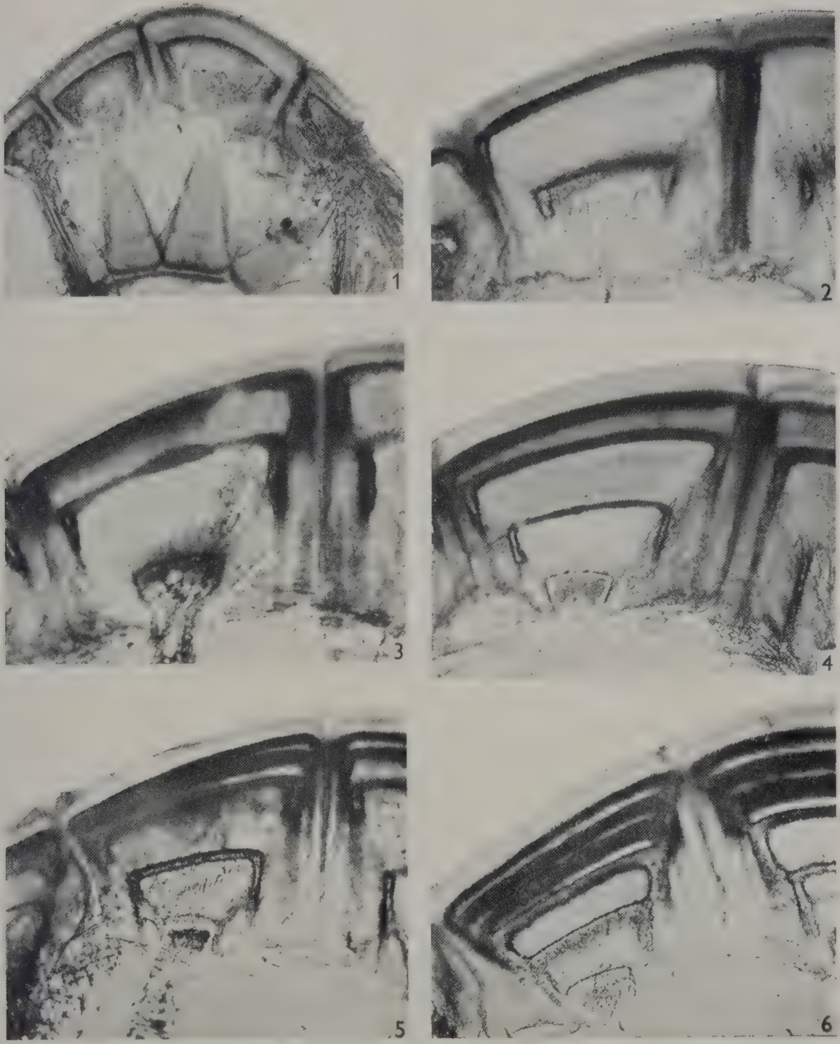
## EXPLANATION OF PLATE I

Plate I. Second radials of *Callionymus lyra*

Fig. 1. Female aged 1+, length 69 mm., April 1949.
Fig. 2. Mature male aged 2+, length 168 mm., March 1949.
Fig. 3. Mature male aged 3+, length 198 mm.
Fig. 4. Female aged 4+, length 185 mm., May 1949.
Fig. 5. Male aged 5+, length 172 mm., Oct. 1949.
Fig. 6. Female aged 6+, length 179 mm., Nov. 1948.



Figs. 1–6.

# ON *CALLIONYMUS RETICULATUS* C. & V. AND ITS DISTRIBUTION IN EUROPEAN SEAS

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(Plates I–III)

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## INTRODUCTION

In the course of a study of the age and growth of the Common Dragonet, *Callionymus lyra* L., a number of specimens of another species of *Callionymus* have been collected off Plymouth, differing from both *C. lyra* L. and *C. maculatus* Rafinesque, the only two dragonets previously recorded from the Plymouth area (Mar. Biol. Assoc., 1931), and, indeed, from northern European seas (Andersson, 1942; Day, 1880–84; Duncker, Ehrenbaum, Kyle, Mohr & Schnakenbeck, 1929; Jenkins, 1925; Mohr (in Joubin, 1929–38); Le Danois, 1913; Norman, 1935; Otterstrøm, 1912; Poll, 1947; Redeke, 1941; Sæmundsson, 1949; Smitt, 1892–95).

Through the kindness of Prof. L. Bertin, Muséum National d'Histoire Naturelle, Paris, who gave me full information about the type specimens of both *C. fasciatus* C. & V. and *C. reticulatus* C. & V., this additional species has been identified as *C. reticulatus* Cuvier & Valenciennes (1837).

Specimens in the collections at the Plymouth Laboratory and from other institutions in Great Britain, and other European countries, have yielded some interesting information about this fish.

## Historical Review of the European Dragonets

Altogether seventeen 'species' of *Callionymus* have been described from European waters. Their names, together with references to the original descriptions, are listed in chronological order below:

| | |
|---|---|
| *C. lyra* Linnaeus | 1758, p. 249. |
| *C. dracunculus* Linnaeus | 1758, pp. 249–50. |
| *C. pusillus* Delaroche | 1809, pp. 330–31; Pl. 25, fig. 16. |
| *C. maculatus* Rafinesque | 1810, p. 25; Pl. V, fig. 1. |
| *C. festivus* Pallas | 1811; pp. 146–47. |
| *C. rissoi* Lesueur | 1814; pp. 5–6; Pl. I, figs. 16, 16*a*, 16*b*. |
| *C. elegans* Lesueur | 1814; p. 6; Pl. I, figs. 17 and 17*a*. |
| *C. belenus* Risso | 1826; pp. 263–64. |
| *C. admirabilis* Risso | 1826; p. 264; Pl. VI, fig. 11. |
| *C. morrissonii* Risso | 1826; pp. 265–66; Pl. VI, fig. 12. |
| *C. lacerta* Cuvier | 1829; pp. 247–48. |
| *C. cithara* Cuvier | 1829; p. 248. |
| *C. reticulatus* Cuvier & Valenciennes | 1837; Vol. 12, pp. 284–85. |
| *C. fasciatus* Cuvier & Valenciennes | 1837; Vol. 12, pp. 285–86. |
| *C. sueurii* Cuvier & Valenciennes | 1837; Vol. 12, pp. 291–93. |
| *C. phaëton* Günther | 1861; p. 147. |
| *C. parthenopoeus* Giglioli | 1883; pp. 397–400. |

In addition, Ninni (1934) described two forms, *C. maculatus atlanticus* and *C. festivus giglioli* (= *C. parthenopoeus* Giglioli, 1883); and Gonçalves (1942) recorded two unidentified species of *Callionymus* from Portuguese waters.

Comparatively few of the above have been accepted, however, by such authorities as Cuvier & Valenciennes (1837), who recognized only six of the earlier species (including Cuvier's two), while at the same time they described three new ones. In 1861 Günther, who made an exhaustive study of the European dragonets, established one new species, *C. phaëton*, and recognized four other good ones—*C. lyra*, *C. maculatus*, *C. festivus* and *C. belenus*. *C. fasciatus* and *C. reticulatus* were considered by him as doubtful species and all the others as synonyms.

*C. fasciatus* was described by Cuvier & Valenciennes (1837) from a single type specimen from Sicily. There was no further record of this species until A. P. Ninni (1877–78) had occasion to examine a number of specimens taken near the Istrian coast. He decided that it was definitely a good species, and worked out a key to the European *Callionymus*, which included the five species recognized by Günther, plus *C. fasciatus*. After A. P. Ninni there were further records of *C. fasciatus*, and its distribution, which is confined to the Mediterranean, was given by Carus (1889–93) and by E. Ninni (1934).

Like Günther, Fage (1918, p. 126) was inclined to think that there are only five good European species. In the same paper he pointed out that *C. parthenopoeus* Giglioli (1883) was a synonym of *C. festivus*, which E. Ninni (1934) redescribed as a form of *C. festivus* Pallas.

The type specimen of *C. reticulatus* Cuvier & Valenciennes (1837) was from Malaga. This species has not been reported since, and has been confused with *C. maculatus* in a number of ways. It was considered as a synonym of *C. maculatus* by Steindachner (1868), Day (1880–84), Carus (1889–93), Smitt (1892–95) and Mohr (in Joubin 1929–38); or identified as *C. maculatus* by Bragança (1903) and Nobre (1935). The descriptions of *C. maculatus* by Moreau (1881) and by Day (1880–84) evidently combined the characteristics of both *C. maculatus* and *C. reticulatus*.

The two unidentified species of *Callionymus* recorded by Gonçalves (1942) are of particular interest (see also p. 302). I was fortunate enough to have the opportunity of examining two specimens, one of each species. One male belonging to the first unidentified species was the identical specimen that had been identified as *C. maculatus* by Bragança (1903) and by Nobre (1935). It proved, however, to be in fact a fully mature male of *C. reticulatus*.

The female specimen belonging to the second unidentified species remains undetermined.

## DESCRIPTION

### **Callionymus reticulatus** Cuvier & Valenciennes

*C. reticulatus* Cuvier & Valenciennes, 1837, Vol. 12, pp. 284–85. *C. maculatus* (part.) Moreau, 1881, Vol. 2, pp. 164, 169–70[1]. *C. maculatus* (part.) Day, 1880–84, Vol. 1, pp. 177–78[1]. *C. maculatus* (nec Raf.) Bragança, 1903, p. 35. *C. maculatus* (nec Raf.) Nobre, 1935, pp. 505–6. *C.* sp. Gonçalves, 1942, p. 80 (fish no. 273, third specimen, male 8·3–11·0 cm.).

*Diagnostic Characters*

(1) The preopercular spine is tricuspid, but occasionally carries a very rudimentary basal spine. (2) The second dorsal fin always consists of ten rays, of which the last is branched. (3) In the second dorsal fin of the adult male there are eight vertical or oblique rows of dark spots. In between these rows of spots there are dark-margined, bluish, tortuous lines and spots. In the anal fin there exist four or five rows of parallel, but discontinuous, dark-margined bluish lines.

*The Plymouth Specimens* (Pl. I, figs. 1–4; Pl. II, figs. 1, 4 and 5; Pl. III, figs. 1–4).

The following description is based on the twenty-one males (40–108 mm.)[2] and fifteen females (30–65 mm.) collected in the Plymouth area during a period of 18 months, from December 1948 to May 1950; and a mature male (the caudal fin had broken, 70 mm. in standard length) collected on 1 August 1900, near Mewstone, Plymouth.

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[1] The descriptions combine the characteristics of both *C. maculatus* and *C. reticulatus*.

[2] The length of the specimens referred to in this paper is total length; except when specific mention is made of standard length.

*General features.* Body of typical dragonet-shape, smooth, devoid of scales and depressed throughout; deepest and broadest in opercular region. Head large, much depressed, and flat on ventral side, contained about 3·2 to 3·6 times (in male) and 3·3 to 3·7 times (in female) in standard length; its width, in opercular region, varying from 1·7 to 2·0 times its depth. Snout spatulate, nearly equal in length to long diameter of eye in females and immature males, but much elongated in mature males. Eyes very prominent, of medium size and closely set on dorsal side; interorbital space very narrow, less than one-half of vertical diameter of eye. Opercular bone very thin; gill opening reduced to foramen; lateral line single, extending to middle of caudal fin, with short branches on trunk and connection with that on opposite side through common dorsal branch near base of caudal fin.

*Fin-rays.* D1, IV; D2, 10; A, 9–10; V, 1, 5; C, 12. First dorsal fin with four flexible spines; second dorsal fin with ten rays, of which first nine are simple but last one is branched twice. Anal fin with nine to ten rays, last ray also branched. Number of fin-rays in dorsal fin very constant.

*Preopercular spines.* The preopercular bone ends posteriorly in three small recurved spines. The anterior and the middle ones are rather stout and curved upwards. The posterior one, which is directed backwards, is much smaller than the other two. It is always less than one-half of the middle one, both in length and in thickness. Among the thirty-seven specimens examined, thirty-four have no free basal spine (i.e. there is no fourth preopercular spine projecting forwards). In the other three, however, the basal spine is distinct but very rudimentary; one has a spine on both sides and the other two have one on the left side only.

*Coloration.* In females and young males the ground colour on the dorsal side varies from orange-brown to orange-red, passing into white or creamy beneath. There are many very light bluish spots scattered over the dorsal side of the body, and six dark orange-red patches along the dorsal median line.

These bluish spots are relatively much larger than those of *C. lyra*, *C. maculatus* and *C. fasciatus*. The six dark, dorsal patches are very similar to those of *C. lyra* and *C. fasciatus;* but in *C. reticulatus* they are very hard in outline, especially the fourth patch which is very characteristic as it has two waves anteriorly and is smooth and rounded posteriorly. On the lateral side of the body there is a series of seven or eight irregular dark spots.

*Sexual dimorphism.* As in many other dragonets, the male secondary sexual characters develop gradually into a state which makes the fully mature male entirely different from the female and the young male in external features. The largest male examined was 108 mm. long, while no mature female exceeded 65 mm.

In the female the first and second dorsal fins are only as high as, or slightly higher than, the body below them, but in the fully mature male they extend to more than three times the body depth. The anal fin, which is less than the body depth in the females, may be nearly twice as high as the body in old males. The lower portion of the caudal fin in the mature male is much longer than the upper portion.

On the second dorsal fin of the male there appear gradually three dark spots, of which the uppermost is always very faint, on the membrane between the consecutive rays. As the spots immediately posterior to the odd-numbered rays are arranged somewhat on the same level, and those posterior to the rays of even number on another level, they form eight oblique or vertical rows crossing the rays diagonally, instead of rows running parallel with the dorsal outline as in the male *C. maculatus* (compare Pl. I, figs. 1 and 3 with Smitt, 1892–95, Pl. XV, fig. 1, reproduced in Pl. 36 of Jenkins (1925) and later editions). In between these rows of dark spots, there are eight rows of dark-margined, bluish, tortuous lines and irregular spots. These lines and spots are more or less continuous in young males. On the anal fin of mature males there are four or five parallel rows of dark-margined, discontinuous bluish lines, which turn obliquely downwards on the membrane between the branches of the last ray. The ventral fin of the mature male becomes very dark and the caudal fin bears many dark-margined, bluish spots and lines. In old males, the ground colour between the spots and lines on all median fins is bright yellow.

### *Other Channel Specimens*

Two young specimens, 31 and 34 mm. long (British Museum Fish nos. 1951.2.19.51 and 52), were collected by the *Manihine* in the English Channel at position 50° 35′ 45″ N., 1° 20′ 40″ E., on 28 August 1949. The smaller of these specimens has a rudimentary basal spine on the preoperculum of the right side.

### *A North Sea Specimen*

One adult male (British Museum Fish no. 1950.11.11.1), 74 mm. long, was contained in a bottle labelled 'Mouth of Thames, Mus. Leach'. William Elford Leach, M.D. (1790–1836), was naturalist assistant librarian, and later assistant keeper, at the British Museum, 1813–21. It would thus appear that this specimen was extant before the species was described as new.

### *A Portuguese Specimen*

Dr H. Vilela, Estação de Biologia Marítima, Lisbon, kindly lent me ten valuable specimens[1] of *Callionymus* collected off the Portuguese coast. One of the specimens, a mature male, 110 mm. long, was identified as *C. reticulatus*

---

[1] A female specimen, 57 mm. long, was collected at the same time and from the same locality as the above male (Gonçalves, 1942, p. 81, Fish no. 274, *Callionymus* sp.). This is a very interesting specimen because the preoperculum has four recurved spines. Like *C. reticulatus*, its second dorsal fin consists of ten rays and there is no basal spine. As none of the European dragonets has four recurved spines, I am uncertain whether this is an abnormality. This specimen remains unidentified. The other eight specimens are all *C. lyra* L.

C. & V., Pl. II, fig. 8. Its colour has been lost; the second dorsal fin consists of ten rays; the preopercular bone has only three recurved spines and no basal spines; the male secondary sexual characters other than coloration are the same as those of the Plymouth specimens. Dr Vilela also informed me that it was collected by Don Carlos de Bragança, the King of Portugal, near Sezimbra (between Cape Espichel and mouth of River Sado), by trawl-net, 110 m. depth, year 1897, and that it is the identical specimen referred to by Bragança (1903, p. 35), Nobre (1935, pp. 505–6) and Gonçalves (1942, p. 80, no. 273, *Callionymus* sp., the third specimen).

### *The Type Specimen*

Prof. L. Bertin has kindly given me the following information about the type specimen of *C. reticulatus* C. & V.:

> Nous avons eu le désagrément de constater qu'il est en très mauvais état. Ses nageoires et sa coloration ne peuvent être connues.
>
> Nous pouvons seulement vous dire que le préopercule comporte seulement 3 épines dirigées vers l'arrière et dont le plus ventrale est presque rudimentaire. Il n'y a pas de 4-ème épine dirigée vers l'avant. C'est à peu près la disposition de votre photographie No. 2 de votre lettre du 9 août.
>
> Dans ces conditions, nous sommes très perplexes au sujet de vos spécimens de Plymouth. Êtes-vous sûr que ce ne sont pas des *C. fasciatus*.—Le type de cette espèce, nous vous le répétons, a 4 épines operculaires.
>
> Fage, dans son travail de 1918, ne parle pas de *C. reticulatus*.

The original description of *C. reticulatus* by Cuvier & Valenciennes (1837) is reproduced here for reference.

> Le Callionyme réticulé.
> (*Callionymus reticulatus*, nob.)
> Elle nous a été donnée par M. Baillon, qui l'a reçue de Malaga. Son museau est un peu plus long et plus pointu que dans le *Callionymus cithara*: il a aussi trois rayons à la pointe du préopercule. Le premier rayon dorsal s'alonge en fil d'un peu plus du quart de la longueur totale. La seconde dorsale n'a pas trois fois la hauteur du corps, et l'anale est de moitié moindre, en sorte que l'une et l'autre est plus basse que dans le *C. cithara*. La deuxième dorsale a un rayon de plus.
> D. 4–10. A. 8, etc.
>
> Il y a sur la seconde dorsale trois rangées de taches brunes semblables à celles du *C. cithara*; mais les intervalles sont remplis de cercles et de rubans ondulés, blancs, avec un liséré mince, brun et blanc; d'où résulte un ensemble très-agréable à l'oeil. La première a deux ou trois de ces rubans ondulés et à double liserés, et deux ou trois taches noires. Quatre lignes semblables, mais plus étroites, parcourent parallèlement toute la longueur de l'anale, dont le bord est noirâtre. Sur l'anale, entre les rayons supérieurs, sont des traits obliques; entre les autres des longitudinaux, tous blancs, lisérés de brun. On voit aussi quelques taches semblables sur la joue et à la base de la ventrale.
>
> La longueur de notre individu est de trois pouces et demi.

In studying all the material mentioned above, I have found that the specimens from different localities are identical with the original description of

*C. reticulatus* C. & V. and Prof. Bertin's information about the type, except in one minor point, which is that there are only eight rays in the anal fin in the type. This is probably due to variation. Different from all other European dragonets, *C. reticulatus* is definitely a good species. The details will be discussed under the heading 'Comparison with other European species'.

## DISTRIBUTION

If the above information concerning *C. reticulatus* be accepted it is clear that this species is present in the western portion of the Mediterranean in Spanish waters off Malaga, and in coastal areas off Portugal, and extends into the English Channel and southern North Sea. Recently there have been reports of the spread of southern forms, notably fish and certain algae, into the northern waters of the European seas and into the Northern Atlantic (Cotton, 1935; Fridriksson, 1949; Lund, 1945; Parke, 1948; Tåning, 1949). It appeared at first that the presence of *C. reticulatus* in the Plymouth area might be yet another example of immigration from the south. It now seems more likely that this species has been overlooked and that it may therefore long have been even more widely distributed in European waters than the above records would suggest.

## ECOLOGICAL NOTES

The catches of *Callionymus* in the Plymouth area during a period of 18 months, from December 1948 to May 1949 inclusive, indicate the great scarcity of *C. reticulatus* as compared with the other two dragonets. Altogether thirty-six specimens of *C. reticulatus* have been caught (30–108 mm. long); but the total number of *C. lyra* (30–300 mm. long) amounts to over four thousand, and that of *C. maculatus* (30–109 mm.) to 149. The nets used were (*a*) the ordinary otter trawl, (*b*) ordinary otter trawl with small-mesh cod-end, (*c*) fine-meshed Agassiz trawl, and (*d*) small beam trawl (shrimp netting). Owing to their small size[1] *C. reticulatus* and *C. maculatus* would not normally be expected in an ordinary trawl catch, and in fact most of the specimens of these two species were caught in the Agassiz trawl and in the small-mesh cod-end of the otter trawl. The relative abundance of *C. lyra* in the catches is therefore probably due to its presence in greater numbers and to the retention of this large species in the ordinary otter trawl. It is interesting to note, however, that on 18 January 1950, ten specimens of *C. reticulatus* were caught in the Agassiz trawl off Whitsand Bay, and at the entrance of Plymouth Sound, from off Wembury Bay and the Mewstone to Whitsand Bay and Cawsand Bay. This represents a total of about 3 hr. trawling by this net, and indicates considerable numbers of this species on these grounds.

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[1] In the Plymouth area *C. reticulatus* reaches at least 108 mm. Although my largest specimen of *C. maculatus* is 109 mm. a preserved specimen of 124 mm. is present in an old collection in the Laboratory of the Marine Biological Association.

Although *C. lyra*, *C. maculatus* and *C. reticulatus* may be trawled from the same grounds in the Plymouth area, it seems that they have their own habitat preferences. *C. lyra*, one of the commonest fishes in this locality, has a very wide distribution. The adults inhabit all the offshore waters off Plymouth. The young fish usually spend the first year very close to the shore and may go as far as 3 or 4 miles up the River Tamar. *C. maculatus*, very scarce inside Plymouth Sound, is sparsely but fairly generally distributed on the trawling grounds off Plymouth. *C. reticulatus*, on the contrary, seems to have a definitely localized distribution in this area. Out of the thirty-six specimens obtained, twenty-seven were caught in or near the entrance to Plymouth Sound, from Wembury Bay to Whitsand Bay, and four from the *Amphioxus* grounds near the Eddystone. Two of the remaining five specimens were obtained from the stomach of a gurnard (*Trigla* sp.). Furthermore, this species does not frequent brackish water as does the young *Callionymus lyra*, and it is very rare in the offshore water on the trawling ground off Plymouth, where *C. maculatus* is common and the adults of *C. lyra* are plentiful.

Unfortunately, no full information about the breeding season has been obtained, but some indications can be derived from the time at which the mature specimens were caught. Among the males there are two specimens with fully developed secondary sexual characters. The first, 72 mm. long, was obtained in May of 1949, and the other, 108 mm. long, collected in 1950, was also obtained in the month of May. Altogether there were four females which could be considered as mature as they contained very large eggs. In the first, 59 mm. long, caught in March 1949, the ova measured up to 0·5 mm. in diameter. The second, 60 mm. long, was obtained in May of 1949, and contained ova measuring up to 0·7 mm., and the third one, 63 mm. long, trawled in May of 1950, contained ova up to 0·5 mm. In another, caught in June of 1949, the ova measured up to 0·4 mm. Several eggs, found lying free in the body cavity of the second mature female, had very large hexagonal reticulations on the vitelline membrane; these reticulations varied from 18 to 26 $\mu$ across. It is obvious from the above that the breeding season of *C. reticulatus* in the Plymouth area extends at any rate from March to June.

## Comparison with Other European Species

As *C. reticulatus* C. & V. shares many important characteristics common to *C. lyra*, *C. maculatus* and *C. fasciatus*, with any one of which it may easily be confused, I examined the most important characters of a number of specimens of these three species from different localities. The details are described below and shown in Table I.

*C. fasciatus* C. & V. Prof. L. Bertin has provided the following information about the type specimen:

> J'ai examiné le type *Callionymus fasciatus* C. & V. Il possède à chaque préopercule 3 épines dirigées en arrière et une épine dirigée en avant, selon le schema ci-dessous, et

TABLE I. COMPARISON OF THE FREQUENCIES OF THE NUMBERS OF PREOPERCULAR SPINES, AND THE NUMBERS OF RAYS IN THE DORSAL AND ANAL FINS OF *CALLIONYMUS RETICULATUS*, *C. FASCIATUS*, *C. MACULATUS* AND *C. LYRA* EXAMINED FROM DIFFERENT LOCALITIES

| | | *C. reticulatus* C. & V. | | | | | *C. fasciatus* C. & V. | | | *C. maculatus* Rafinesque | | | | *C. lyra* L. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Malaga (Type) | Plymouth | English Channel | Southern North Sea | Portugal | Sicily (Type) | Genoa | Istria | Port Vendres | Plymouth | Port Erin | Mill-port | Plymouth | Port Erin | Portugal |
| No. of rays in the dorsal fins | IV+8 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 4 | .. | .. |
| | IV+9 | .. | .. | .. | .. | .. | .. | .. | .. | 4 | 107 | 5 | 6 | 277 | 39 | 8 |
| | IV+10 | 1 | 37 | 2 | 1 | 1 | 1 | 2 | 2 | .. | 2 | 1 | .. | 1 | .. | .. |
| No. of rays in the anal fin | 8 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. | 4 | 1 | .. |
| | 9 | .. | 36 | 2 | 1 | 1 | 1 | 2 | 2 | 4 | 105 | 6 | 6 | 278 | 38 | 8 |
| | 10 | .. | 1 | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. | .. | .. | .. |
| Preoperculum with three recurved spines and | A basal spine: Well-developed | .. | .. | .. | .. | .. | 1 | 2 | 2 | 4 | 109 | 6 | 6 | 282 | 39 | 8 |
| | A basal spine: Rudimentary | .. | 3 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| | No basal spine | 1 | 34 | 1 | 1 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |

répondant à peu près à la disposition de votre *C. maculatus* (Photo N. 3). La 3e épine est cependant un peu plus courte et la 4e est moins détachée de l'os préoperculaire.

La coloration de la seconde dorsale—il s'agit d'un mâle—est différente de celle de votre photographie No. I. Il y a en effet 3 ou 4 taches noires dans chaque espace interradiaire, au lieu de 2 ou 3. Le nombre des rangées de ces taches est donc plus élevé que sur votre photo et rappelle la disposition du *C. maculatus* dessiné par Erna Mohr dans la fiche de la Faune ichthyologique de l'Atlantique Nord.

Sur la première dorsale, il n'y a pas de tache prédominante, mais la disposition figurée ci-dessous:

Je ne connais pas le fig. 2. pl. 40 dont parlent Cuvier et Valenciennes.

*C. fasciatus* me semble tomber en synonymie avec *C. maculatus*. C'est d'ailleurs l'opinion déjà soutenue par Fage, dans un très important travail que vous semblez ignorer: Shore-Fishes, dans Report Danish Oceanogr. Exped. Medit. Adj. Seas-Vol. II- Biology-A. 3. paru en 1918.

Reste à savoir ce que sont vos spécimens ayant seulement 3 épines préoperculaires (et quelquefois 4).

D'après Fage et les auteurs consultés il n'existe dans la Manche et l'Atlantique que *C. lyra* et *C. maculatus* (*fasciatus*) qui ont toutes deux 4 épines.

Les espèces à 3 épines n' existent qu'en Méditerranée.

Il y a donc là un point à éclaircir, mais sur lequel je ne puis vous rendre aucun service à distance.

The four specimens of *C. fasciatus* belonging to the 'Museo Civico de Storia Naturale, Genova', comprise three mature males and one female. The first male was from 'Golfo di Genova' (71[1]) mm. long; the second and third males were from 'Istria', 83 (66[1]) mm. and 90 (71[1]) mm. long respectively (Fish nos. 265A, 468*a*); and the female, from 'Golfo di Genova', was 55 (44) mm. long (Fish nos. 265, 486). D 1, IV; D 2, 10; A, 9; V, 1, 5. The last rays of both the second dorsal and the anal fin are branched. The preopercular bone has always three recurved spines and a very prominent basal spine (Pl. II, figs. 6, 7). There are four dark spots on the membrane between consecutive rays in the second dorsal fin, and the spots on the fin are also arranged in oblique or vertical rows across the fin as in *C. reticulatus*. There are six to eight rows of dark-margined, bluish parallel lines in the anal fin of the male.

*C. lyra*. Altogether 329 specimens were examined, the length of the specimens varying from 40 mm. to about 300 mm. They all have four very prominent preopercular spines, three recurved spines and a basal spine. The number of the second dorsal fin-rays varies from eight to ten (Pl. I, fig. 5; Pl. II, fig. 3).

*C. maculatus*. I have examined 125 specimens from different localities. The preopercular bone has constantly four spines. On the second dorsal fin of the males there are four horizontal rows of dark spots; sometimes there are similar numbers of light round spots lying immediately behind the dark spots. There are no parallel lines on the anal fin such as are found in *C. fasciatus* and

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[1] The figures in brackets are standard length. The total length of one of the specimens is not known as the tail has been damaged.

*C. reticulatus*. Dark round spots are present on the sides of the body (Pl. I, fig. 6; Pl. II, fig. 2).

*C. reticulatus* C. & V. can therefore be distinguished from *C. lyra*, *C. maculatus* and *C. fasciatus* by the following characteristics:

(1) The preopercular spines are the most reliable characteristic. In *C. reticulatus* there are three recurved spines, which project upwards or backwards; but the basal spine, which projects forwards, is normally absent. If present, it is very rudimentary (Pl. II, figs. 4, 5) and is usually on one side only (p. 300). In the other three species, however, there are also three recurved spines, but the basal spine is always present and very prominent (Pl. II, figs. 2, 3, 6 and 7).

(2) The number of the fin-rays in the second dorsal fin is constantly ten in *C. reticulatus* and in *C. fasciatus;* in *C. lyra* and *C. maculatus*, however, there are normally nine rays, but occasionally eight or ten rays. The last rays of the second dorsal fin of all these four species are branched.

(3) The colour patterns on the body of *C. reticulatus* are very similar to those of *C. fasciatus* and of the young *C. lyra*. Nevertheless, in the first species the light bluish spots are much larger than those in the latter two species, in specimens of similar size. As a rule the dorsal patches of *C. maculatus* and *C. lyra* have irregular margins, whereas those of *C. reticulatus* have always very well-defined entire margins, especially the fourth which is very characteristic (Pl. I, figs. 2 and 4–6). As *C. maculatus* has dark spots on the sides of the body, there can be no difficulty in distinguishing it from the other three species, so long as these spots have not been lost in preservation.

(4) The male secondary sexual characters are very different in the mature adults of these four species. There can be no difficulty in distinguishing them when the specimens are fresh, or in preserved material, if the coloration has not been lost completely. The smallest mature male of *C. lyra* is about 180 mm. long. Its greatly elongated first dorsal fin may extend to the base of the caudal fin or beyond it. There are no dark spots on the first and the second dorsal nor on the anal fin (Couch, 1863, pl. CIII; Holt, 1898, pl. XXVI; Jenkins, 1925, pl. 34; Smitt, 1892–95, tab. XIV). The mature males of *C. maculatus*, *C. fasciatus* and *C. reticulatus* are much smaller in size (see pp. 299 and 306). On the second dorsal fin of these three species there are dark spots on the membrane between consecutive rays—four spots in *C. maculatus*, four (the uppermost very faint) in *C. fasciatus*, and three (the uppermost also very faint) in *C. reticulatus*. In *C. maculatus*, these dark spots are arranged in more or less horizontal rows (Smitt, 1892–95, tab. XV, fig. 1; Günther, 1867, pl. V, fig. A; E. Ninni, 1934, tab. II and III, fig. 1). In *C. fasciatus* and *C. reticulatus* these spots are arranged in oblique or vertical rows (Guérin-Meneville, 1829–44, pl. 40, no. 2; E. Ninni, 1934, pl. III, fig. 2; and Pl. I, figs. 1 and 3 in this paper). Furthermore, in both *C. fasciatus* and *C. reticulatus* there are rows of bluish dark-margined, tortuous lines or spots on the second dorsal fin; and

dark-margined bluish parallel lines on the anal fin. In the former there are six to eight lines; while in the latter there are only four or five lines.

As regards the other three European dragonets, *C. phaëton* has two recurved spines, but *C. festivus* and *C. belenus*, like *C. reticulatus*, also have only three recurved spines. Nevertheless, the dorsal fins of *C. belenus* and *C. festivus* have fewer rays than *C. reticulatus*. The fin formula is D1, IV and D2, 6–7 in *C. festivus*; and D1, III, and D2, 8, in *C. belenus*.

Thus *C. reticulatus* is well distinguished from all other European species, with the possible exception of *C. fasciatus*. These two species present the following incomplete contrasts:

*C. reticulatus*: preoperculum with three recurved spines; rarely a fourth (basal) spine on one or both sides.
*C. fasciatus*: preoperculum with three recurved spines and a strong basal spine.
*C. reticulatus*: mature males with three dark spots on an inter-radial membrane of D2 and four or five horizontal bands on the anal.
*C. fasciatus*: mature males with four dark spots on an inter-radial membrane of D2 and six to eight horizontal bands on the anal.
*C. reticulatus*: distributed from Malaga to the North Sea.
*C. fasciatus*: not known outside the Mediterranean.

The only well-authenticated specimen of *C. reticulatus* from the Mediterranean is the type, but its colour is not known.

The question of geographical variation arises. Fishes with rows of spots on the fins increase the number of rows as the fish grows. The number of mature males of these two species examined by me is too small to admit of generalization, but those named *fasciatus* are not all larger than those assigned to *reticulatus*. In some other species of the northern hemisphere, however, the northern members are known to grow larger and to mature later than the southern, and it is possible that we have here a difference associated with rate of growth. This could hardly account, however, for the presence in one and rarity in the other of a basal spine on the preoperculum; until, therefore, the Mediterranean populations are better known it seems wise to recognize both *C. reticulatus* and *C. fasciatus* as distinct species.

## SUMMARY

Three species of *Callionymus* are recognized as occurring in British waters, *C. lyra* L., *C. maculatus* Raf. and *C. reticulatus* C. & V.

The third is here recognized for the first time and is described from an abundant material.

Both *C. reticulatus* and *C. fasciatus* C. & V. in the past have been confused with *C. maculatus*. They are here shown to be quite distinct from that species.

*C. reticulatus* is closely related to *C. fasciatus*. The value of the characters used to distinguish them is discussed.

## ACKNOWLEDGEMENTS

I am greatly indebted to Mr F. S. Russell, F.R.S., and to Mr G. A. Steven, F.R.S.E., for much help and stimulating criticism during the whole course of this work; to Dr E. Trewavas and Mr D. W. Tucker of the British Museum (Nat. Hist.) from whom I have received invaluable help and much practical advice in the preparation of this paper; to Mr A. Fraser Brunner for preparing the coloured plate; and to Dr D. P. Wilson for the photographs of living specimens. My best thanks are also due to Prof. L. Bertin, Museum National d'Histoire Naturelle, Paris, who kindly examined the type specimens of both *C. reticulatus* and *C. fasciatus* for me; to Dr A. M. Ramalho and Dr B. Velila, Estação de Biologia Maritíma, Lisboa, who supplied important references and loaned valuable specimens; and to Dr D. Guiglia, Museo Civico de Storia Naturale, Genoa, who kindly sent the Mediterranean specimen of *C. fasciatus* for examination.

It is a pleasure to acknowledge assistance from Mr M. D. Menon who collected the valuable specimens from Port Venders; from Dr F. de P. Navarro, Instituto Español de Oceanografía, Madrid; Prof. E. Tortonese, Istituto e Museo de Zoologia dell' Università, Turin; Dr A. Spartà, Istituto Talassografico de Messina, Sicily and Dr T. Šoljan, Institut za Oceanografiju i Ribarstvo F.N.R., Split, Jugoslavia for many references and much information. Mr E. Ford (Millport), Mr J. M. Dodd (St Andrews), Mr J. R. Bruce (Port Erin), and Dr H. O. Bull (Cullercoats), all helped by sending specimens from different British localities for examination. To Dr J. S. Alexandrowicz and Dr H. G. Vevers I am indebted for translations of difficult papers in various languages, and to Dr M. Parke and Mr P. G. Corbin for much general help.

Finally, I have the greatest pleasure in recording my gratitude to the British Council and to the Trustees of the Ray Lankester Fund for the financial assistance without which this work could not have been done, and to the Editor of *Endeavour* for making possible the reproduction of Plate III.

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## EXPLANATION OF PLATES

### PLATE I, photographs of *Callionymus*, × ⅔

Fig. 1. *C. reticulatus* C. & V., mature male, lateral view of a preserved specimen collected in May 1950, Plymouth.

Fig. 2. Same as fig. 1, dorsal view.

Fig. 3. *C. reticulatus* C. & V., male, lateral view of a living specimen collected in November 1949. Plymouth.

Fig. 4. *C. reticulatus* C. &. V., mature female, dorsal view of a fresh specimen collected in July 1950, Plymouth.

Fig. 5. *C. lyra* L., young female, dorsal view of a fresh specimen collected in September 1950, Plymouth.

Fig. 6. *C. maculatus* (Rafinesque), mature female, dorsal view of a fresh specimen collected in May 1950, Plymouth.

### PLATE II, photographs of *Callionymus*, figs. 1–7, × 6·7; fig. 7, × ⅔.

Fig. 1. The right preopercular bone, lateral view, of a male *C. reticulatus*, 86 mm. long, Plymouth, bearing three recurved spines only.

Fig. 2. The right preopercular bone, lateral view, of a male *C. maculatus*, 86 mm. long, Plymouth, showing three recurved spines and one basal spine.

Fig. 3. The right preopercular bone, lateral view, of a female *C. lyra*, 86 mm. long, Plymouth, showing three recurved spines and one basal spine.

Fig. 4. The right preopercular bone, lateral view, of a male *C. reticulatus*, 60 mm. long, Plymouth, bearing three recurved spines and one rudimentary basal spine.

Fig. 5. Same as the above specimen, dorsal view to show three recurved spines and the rudimentary basal spine.

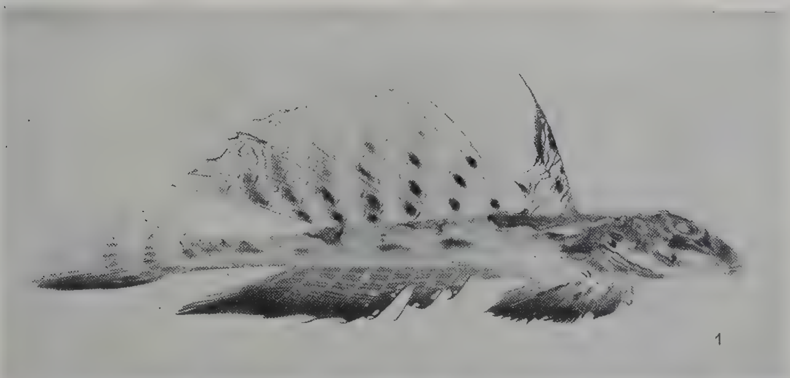
Fig. 6. A portion of the right preopercular bone, dorsal view, of a male *C. fasciatus*, 71 mm. in standard length, Genoa, showing the well-developed basal spine.

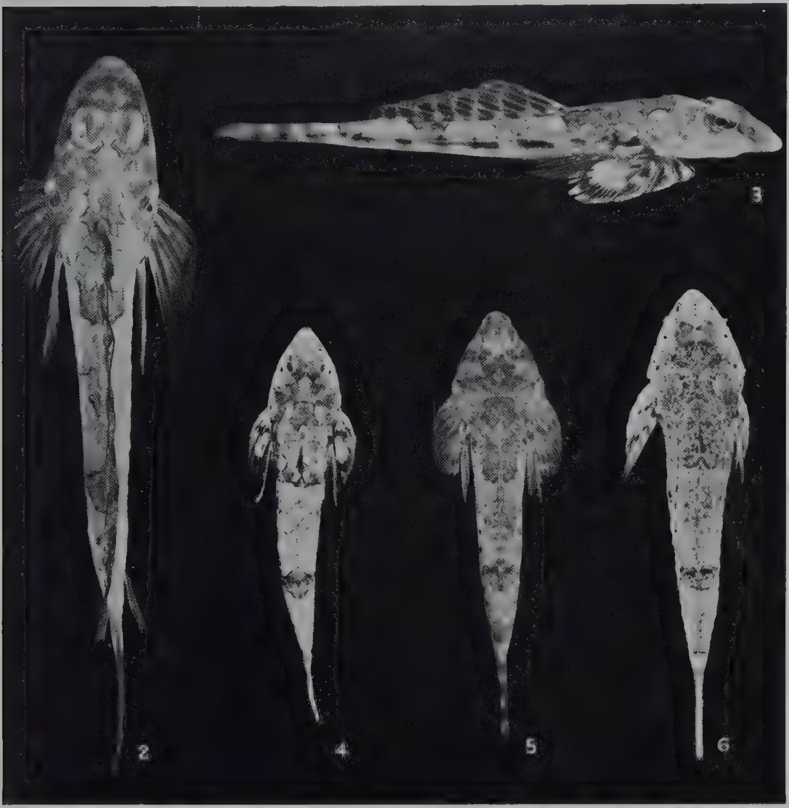
Fig. 7. Same as above, lateral view.

Fig. 8. *C. reticulatus* C. & V., lateral view, mature male, 110 mm. in total length, Portugal.

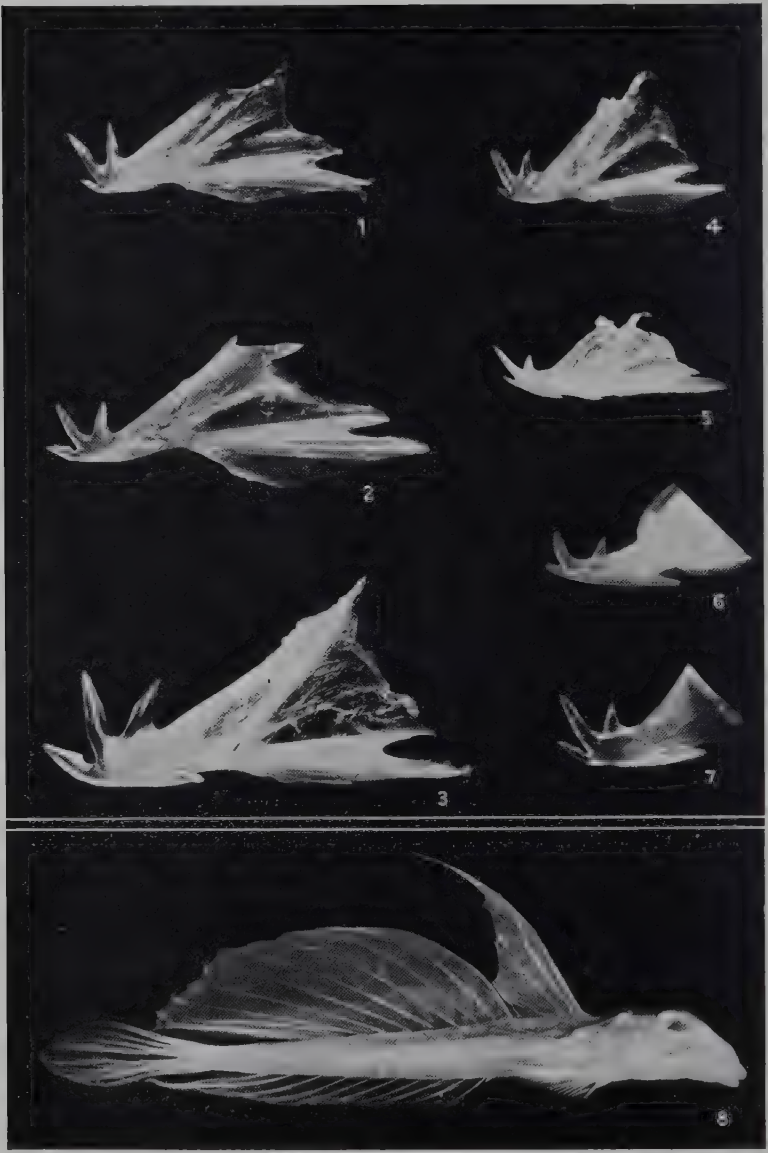
### PLATE III, *Callionymus reticulatus* C. & V.

Figs. 1, 1*a*, male; Figs. 2, 2*a*, female. Fig. 1 is a specimen 108 mm. long caught off Plymouth on 11 May 1950. (*From original coloured drawing by A. Fraser Brunner.*)

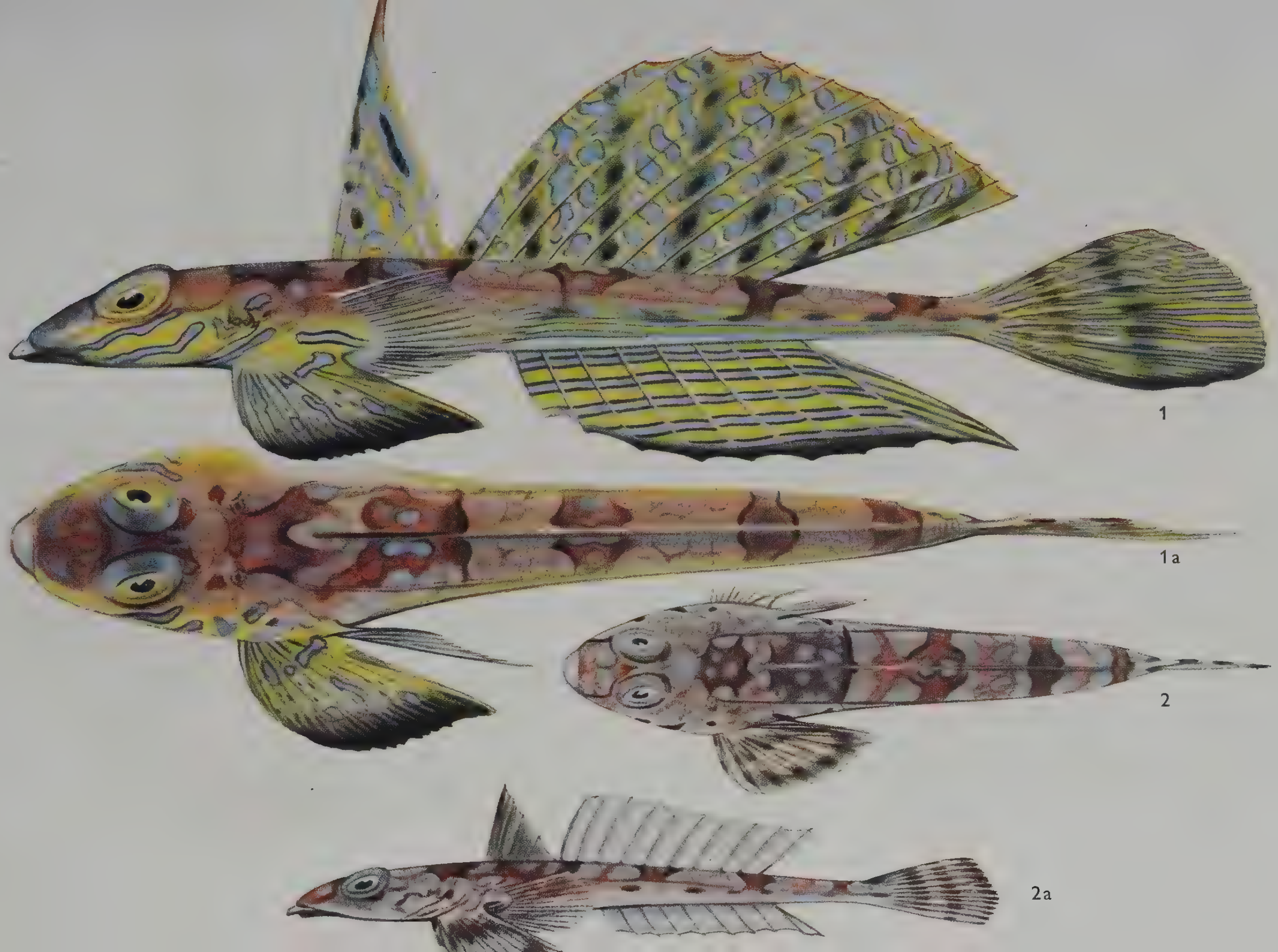




Figs. 1–6.



Figs. 1–8.


1
1a
2
2a

# A RE-EXAMINATION OF *CALANUS* COLLECTED OFF PLYMOUTH

By F. S. Russell, F.R.S.
Director of the Plymouth Laboratory

Rees (1949) has established significant biological differences between the two forms of the copepod *Calanus finmarchicus*, namely *finmarchicus* and *helgolandicus*. It is therefore necessary that in future research on the behaviour of *Calanus* the two forms should be distinguished.

I have myself published observations on the vertical distribution of *Calanus* and on the seasonal changes in size of individuals of the populations of this copepod off Plymouth. In order to know whether my results have been vitiated by the presence of the two forms in the collections, I have re-examined representative samples of adult females, using the fifth leg as the distinguishing character. The collections in question were those made in 1926 which formed the subject of a paper on seasonal changes in vertical distribution and in the sizes of individuals of different generations (Russell, 1928); and those made in 1931 and recorded in my paper on the vertical distribution of *Calanus* in relation to light intensity (Russell, 1934).

From the collections made between April and September 1926, twelve samples amounting to 240 individuals were examined. Among these, eight specimens were *finmarchicus*, the remainder being *helgolandicus*. The form *finmarchicus* only occurred in the months April, May and June, the maximum number in any one sample being 10 %. Over 300 specimens were examined from the collections made in July and August 1931; all were *helgolandicus*.

I have also examined over 200 specimens scattered through the collections made in 1930 on which the results reported by Bogorov (1934) on seasonal changes in biomass were based. Again *helgolandicus* was found to be similarly predominant. The very large catch recorded on 15 May 1930 (Russell, 1933) contained 4 % *finmarchicus*.

It is thus clear that these published results can be regarded as representative of *helgolandicus*, and the vertical distribution and seasonal changes refer to that form. It is interesting to record that the only specimens of *finmarchicus* occurring in May, in 1926 and 1930, were much smaller than the *helgolandicus* which attained their greatest size in that month. Rees (1949) similarly found *finmarchicus* to be smaller than *helgolandicus* in the North Sea.

I am grateful to Dr C. B. Rees for confirmation of some of my identifications.

## SUMMARY

A re-examination of some collections of the copepod *Calanus finmarchicus* made off Plymouth has shown that the conclusions reported in the following publications can be regarded as referring to the form *helgolandicus*.

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# LYMPHOCYSTIS TUMOURS IN THE RED MULLET (*MULLUS SURMULETUS* L.)

By J. S. Alexandrowicz

From the Plymouth Laboratory

(Plates I–IV)

A specimen of the red mullet (*Mullus surmuletus* L.), caught in Plymouth waters in October 1949, was found to have tumours projecting externally on the pectoral fins. They were spherical or elliptical in shape, the largest being 20 mm. long. On the suggestion of Mr G. A. Steven some of these outgrowths were cut out and given to the writer for microscopic examination.

When examined fresh they appear to consist of small, spherical, cyst-like bodies of various diameters, but there was no obvious clue as to their nature. After fixing in Bouin and sectioning, they are seen to be composed of cells of various sizes (Pl. I, figs. 1–4). It can be seen that these cells lie close to one another, leaving only a little space for the embedding connective tissue which is characterized by the abundance of its own small cells. The blood vessels met with in this tissue contain fish erythrocytes. The whole is covered by stratified squamous epithelium (Pl. I, fig. 2).

The cells of the tumours have large nuclei very much like those of egg cells, and this resemblance is made still greater by the presence of a distinct cell membrane. On the other hand, they show certain peculiarities which do not occur either in ova or in other cells of normal tissues, viz. their cytoplasm includes bodies in its peripheral layer which stain readily with chromatin stains. Examined under higher power these bodies appear as a network of bars of different shapes, including alveolar spaces, the peculiar arrangement of which can be better seen in tangential sections (Pl. IV, fig. 20).

Although there are certain differences in the appearance of the cells of different sizes, there can be no doubt that they all represent successive stages of development of the same elements growing from the inconspicuous size of a few microns up to giant cells of more than 400 $\mu$ in diameter. During this development critical stages must be of common occurrence as many of the cells are obviously in a state of degeneration.

From this description it is clear that these tumours are those characteristic of the lymphocystis disease known to attack various fresh-water and marine fishes, but, apparently, not yet recorded in the red mullet.

The term 'lymphocystis' is a misnomer in both components of the word and may evoke a totally wrong idea as to the nature of the disease; it originates from the time when the cells of these outgrowths were mistaken for parasitic

Sporozoa. The history of the subject is an unusual one, for the peculiar aspect of the cells gave rise to another erroneous assumption that they were eggs laid by some animal under the skin of the fish.

Weissenberg (1914) was the first to recognize that these cells were hypertrophied fibroblasts of the fish itself, and Joseph (1918) came to the same conclusion independently. To Weissenberg goes also the merit of proving experimentally, in his earliest researches on the pike perch (*Acerina cernua*), the infective nature of this disease; he was able to confirm this later on some American fishes (*Stizostedion vitreum*, *Lepomis macrochirus* and *L. gibbosus*).

The bibliography of the subject and a list of species in which the lymphocystis disease has been described are given by Nigrelli & Smith (1939); recent additions have been supplied by Weissenberg (1945). The following species from European waters are so far recorded with the disease: *Pleuronectes flesus*, *P. platessa*, *Acerina cernua* and *Sargus annularis*.

The first data on the characteristic microscopical structure of the lymphocystis tumours have been given by Woodcock (1904). The most detailed histological investigations have been made by Joseph (1918) and Weissenberg (1920). The problem of the nature of the virus responsible for the disease has been touched upon in one of the later papers by Weissenberg (1945).

Among the established characteristics of the disease attention may be drawn to the following. The tumours may grow not only on the skin but also in the internal organs (mesentery, intestine, ovary and spleen). There has been observed a certain periodicity in the development of the disease marked by the eruption of new tumours; it has also been ascertained that the infected fishes can overcome the disease after a longer or shorter period of time and that their skin may resume quite a normal appearance.

It is generally admitted that the disease is due to a virus, although positive proof by virus-test methods has apparently not yet been given. This virus has not proved to be identical in every instance, for in Weissenberg's experiments on *Acerina cernua* and *Stizostedion vitreum* only those fishes belonging to the same species could be infected and he, therefore, assumed that the virus was species-specific. This assumption was, moreover, in agreement with the observations of other investigators that other species of fishes kept for a long time in the same tank with the infected species did not develop similar tumours. However, in 1945, Weissenberg succeeded in transmitting the infection from the bluegill (*Lepomis macrochirus*) to the common sun fish (*L. gibbosus*).

## SOME FEATURES OF THE LYMPHOCYSTIS TUMOURS IN *MULLUS SURMULETUS*

On *macroscopic* examination alone one might hesitate to identify the tumours found in the red mullet with those observed by previous writers. In their descriptions and illustrations the lymphocystis tumours are represented as numerous small disseminated swellings which, if united into larger bodies, distinctly show their composite structure. Raspberry-, mulberry- and cauliflower-like outgrowths are the terms used to give an idea of their shape. Weissenberg alone mentions that some of them may have a smooth surface.

In *Mullus* no such disseminated nodules were met with, and the few tumours (five in all) had rather smooth surfaces. Only one of them, situated at the corner of the mouth, was comparatively small, being 3 mm. in diameter; the dimensions of the others ranged from 9 to 20 mm.

*Microscopically*, the lymphocystis cells in *Mullus* show the same characteristic features already recorded in other species, and they closely resemble those of *Sargus annularis*. Many of the details are so much alike that several of Joseph's photomicrographs might have been made from my preparations of *Mullus*. In view of these similarities, it seems superfluous to describe every detail, as they have been discussed at length by Joseph and by Weissenberg. I therefore intend to concentrate only on those points which have given rise to controversy in the past, or which have apparently not been observed in the species previously investigated.

## EARLY STAGES OF THE LYMPHOCYSTIS CELLS AND THE DEVELOPMENT OF THE INCLUSION BODIES

Although in their later stages all the lymphocystis cells look alike, according to Joseph they may have a double origin: some develop from the 'basiepidermoidale Zellen', cells situated in the epidermis, others from the connective tissue elements, especially from the osteoblasts. He thought that the inclusion network originated in the former cells from a dark-staining body noticeable even in very small (*c.* 8 $\mu$) cells; and in the latter he first observed it in the cells which had reached *c.* 30 $\mu$ in diameter, in the shape of a small 'calotte' which quickly grows around the nucleus and becomes transformed into a network, moving later into the cortical layer of the cytoplasm.

On the basis of his own observations, as well as on theoretical grounds, Weissenberg rejects the possibility of lymphocystis cells developing from the epidermis elements. He admits their origin from the connective tissue cells and gives a detailed account of the very earliest modifications of the latter as they begin their transformation into the lymphocystis cells.

The origin of the inclusion bodies in the tumour cells of *Acerina cernua* is described by him as follows: 'At first they contained no inclusion body. But about one week later, an inclusion appeared in their cytoplasm as a tiny point which increased in size to a round compact body resembling very much a Guarnieri body of a corneal epithelium cell of a rabbit after inoculation with vaccine virus. The young lymphocystis cells grew larger and larger and corresponding to their growth the inclusion body increased more and more in size to an oval disc, then to a calotte, which became fenestrated and sprouted into a network of basophilic staining reaction.'

Later investigations by the same writer on various species confirmed his conclusions about the origin of the lymphocystis cells and their inclusion bodies. In every instance the latter were found appearing first as one, or sometimes several, small granules, which in some species could be seen in the youngest stages of the tumour cells. When, however, Nigrelli & Smith (1939) examined a lymphocystis tumour of the orange filefish (*Ceratacanthus schoepfii*) they found features to which the following interpretation was given: 'Certain early stages ($9 \times 24\,\mu$) show cells in what resembles a binuclear condition. In other cells ($20 \times 50\,\mu$) the nuclear material appears in two forms: (*a*) as a deeply pycnotic primary nucleus of the enlarged cell, and (*b*) a secondary nuclear mass, variable in size, which becomes vacuolated and reticulated. The later mass of basophilic material represents probably the forerunner of the system of inclusion bodies which eventually become distributed in the cytoplasm of the enlarged older cell ... .'

The aspect of these cells has therefore much in common with those lymphocystis cells in *Sargus annularis* which Joseph saw developing at the basis of the epidermis, and which contained, apart from the nucleus, another body of such conspicuous dimensions that Joseph said that he hesitated to decide which of these bodies might be the genuine nucleus. But while Joseph lays stress on the point, on which he and Weissenberg are quite unanimous, that the elements of the future inclusion network do not migrate from the nucleus, Nigrelli & Smith suggest that these inclusions may originate from 'one or two nuclear masses formed in certain early stages of the disease'.

My own observations have been made on material less suitable for investigating the origin of the lymphocystis cells than if it had been obtained by experimental transmission of the disease, permitting the evolution of the infected cells to be followed from the very first manifestation of the infection. Nevertheless, the tumours of the red mullet, although they were obviously of long standing, included such a variety of stages that a whole series of them could be established even in the same preparation.

The earliest stages are rather scarce, and were found as single elements, or in small groups in some sections only. The largest of the observed nests is represented in Pl. I, fig. 3.

In this connexion it may be pointed out that the occurrence of all stages of development would favour the assumption that a frequent infection of the host cells has been taking place. On the other hand, since large parts of the tumours are composed of cells of equal size markedly differing from neighbouring areas (Pl. I, fig. 1), it is obvious that they belong to the various eruptive periods of the disease. Hence it seems probable that in the *Mullus* tumours both processes were occurring, viz. a frequent infection of a few cells, and periodical exacerbations of the disease producing simultaneous growth of a greater number of the hypertrophic elements. The smallest cells which could be distinguished with certainty as early stages of lymphocystis cells measured 9 $\mu$ in diameter (Pl. II, fig. 6*a*). They can be recognized by their rounded shape, the deeper staining of their cytoplasm, and, more certainly, by their large spherical nuclei of vesicular appearance, each containing a big nucleolus. There are even smaller cells which, compared with the fibroblasts, show modifications tending in the same direction (Pl. II, fig. 5*a*) and which may be regarded as earlier stages, but the same degree of certainty as to their character cannot be claimed.

In all preparations observed the young stages of the lymphocystis cells appear to originate from among the connective tissue elements. No evidence has been met to support Joseph's contention that the lymphocystis elements evolve from two different kinds of host cells.

The appearance of the next stages of the growing cells may be seen in Pl. II, figs. 5–11. Some of them, if cut at suitable angles, distinctly show a large area of the cytoplasm staining more lightly (called 'sphere' by Joseph).

The inclusion bodies in the young cells have the same appearance as figured by Weissenberg, i.e. of granules surrounded by a halo. The inclusions in this Guarnieri-body stage are found so often to be 3, 4 or even 5 in number that their multiple occurrence seems to be the rule in the red mullet. If one traces the evolution of these bodies retrogressively to the smallest cells, one may see the granules diminishing in size and their halos becoming very faint. In Pl. II, fig. 5*b*, five such granules are present but they are not clearly in focus in the photograph. In the smallest cells the granules are at the limits of visibility. Although there must, of course, be uncertainty as to the nature of elements of so small a size, there are reasons for believing that, even in the smallest lymphocystis cells of the red mullet, the substance of future inclusion networks is already accumulating in particles of microscopical dimensions.

The multiplicity of the inclusions in the early stages of the lymphocystis cells was observed by Weissenberg to be a constant feature in some fishes (Pleuronectidae and *Lachnolaimus*), and in them each of these granular bodies was developing into a fragment of the network; in other species investigated by the same author (*Acerina* and *Stizostedion*) additional granules appeared occasionally but remained rudimentary.

Whether or not some of the initial granules seen in the cells of *Mullus* are disintegrating is difficult to determine, and the diminution in their number may be explained as being, at least partly, brought about by the fusion of two or more into one larger mass. The pictures seen in Pl. II, figs. 8–11, may be best interpreted as the successive stages of this process. In Pl. II, fig. 11, the larger inclusion seems likely to be composed of three granules about to fuse into one. Similar lobed outlines of the inclusions can be observed only in the cells belonging to the same range of size in which the fusion of these bodies is occurring; they cannot be regarded as the beginning of the later changes of the inclusions, since these do not set in until the cells grow a good deal bigger.

Cells with a 'secondary nuclear mass', as described by Nigrelli & Smith, have not been found. Only in some cases there could be seen a pycnotic conglomeration of the inclusions producing a body of roughly spherical shape, but these cells were unmistakably in a state of degeneration. Binucleated cells are not uncommon, but their nuclei have an identical and typical appearance, and there is not the slightest evidence that one of them may give rise to the inclusion network. I am therefore in agreement with Joseph and Weissenberg in refuting the theory of the migration of the inclusion substance from the nuclei.

The different organization of the younger stages of lymphocystis cells in the orange filefish as described by Nigrelli & Smith would appear anomalous in view of the resemblance of the later stages of the same cells in various species of fish. It seems, however, that this may be explained as follows. From all we know, the infective agent, after penetrating the host cells, will bring about two processes, viz. the hypertrophy of the cells and the development of the inclusion networks; the latter being most probably, as has been postulated by Weissenberg, the aggregation of the virus substance. In the majority of the species investigated the hypertrophy of the cells sets in before the inclusion bodies become visible; if the reverse should occur, as might be the usual course in the species observed by Nigrelli & Smith, the inclusion body would attain a more advanced stage of development in the comparatively small cell. If this suggestion holds good, it is to be expected that in the orange filefish also, if suitable stages of the disease happen to come under investigation, such Guarnieri-like bodies will be found in the small cells.

*Centriols.* Owing to the multiple occurrence of the inclusion bodies, their variable size and their situation in different regions of the cells, recognition of the centriols described by Joseph in *Sargus annularis* is very uncertain. Some small granules in the lighter part of the cytoplasm, Joseph's sphere, might well be centriols, but in other cases at the same places the granules are of such size that their centriol nature is highly improbable and they are, more likely, to be reckoned among the additional inclusion bodies.

## Further Stages of the Development of the Lymphocystis Cells

### *Inclusion bodies*

The development of the inclusion bodies will be considered first, not only because their changes are the most striking feature in the growing lymphocystis cells, but also because they have an obvious bearing on the organization of the cytoplasm.

The changes in the form of the inclusion bodies, which up to now have retained their characteristic appearance of Guarnieri bodies, become noticeable in the cells of *c.* 50 $\mu$; the oval body becomes flattened and assumes the form of a calotte which starts to expand around the nucleus, undergoing at the same time a transformation into a framework made up of irregular bars. The shape of the body during this process is often far from symmetrical: the calotte may be elongated in one direction, some bars of the framework may extend towards the nucleus, others towards the periphery of the cell, so that in the sections they may be seen scattered through the whole cytoplasm. The independence of some fragments makes it probable that some of them may develop from additional inclusion bodies. With the growth of the cells a more orderly arrangement takes place, and eventually the whole inclusion body represents a hollow sphere, the walls of which are irregularly fenestrated. In the sections it appears as a ring made up of several fragments and situated between the nucleus and the periphery of the cell. As the diameter of this spherical basketwork grows faster than that of the cells, the inclusions soon reach their cortical zone, a position maintained during the subsequent life of the cells.

The development of the inclusions and their definite arrangement in *Mullus* may be defined as being of *Sargus* type, as it is much like that described by Joseph for that fish. It differs greatly from what may be called the *Pleuronectes* type which, according to Weissenberg, consists of numerous inclusion networks densely filling the whole cytoplasm; it differs also, but to a lesser degree, from those of other species investigated by the same author.

The extent of the break-up of the framework in any one cell into separate fragments is difficult to ascertain unless all the serial sections of a given cell are examined. In tangential sections one can see how thin may be the connexions between the bars and, moreover, how different the inclusions of the same cell segment may appear if the sections are made in different planes (Pl. IV, fig. 20).

From the stage at which they reach the periphery of the cells up to the time when the latter grow to their maximal dimensions, the inclusion bodies do not show marked differences in their structure. In the large cells the bars are somewhat more widely spaced, but even then their total mass in any one cell must grow as the cell increases in diameter.

In the cells at the peak of their development the inclusions often appear divided into more fragments and show certain changes: the outlines of the bars become more rounded and their structure shows less fine pattern. These changes may be considered as leading to the degeneration of the inclusion bodies which will be discussed later.

It may be mentioned that the staining reactions of the inclusions confirm Weissenberg's opinion that, besides their main basophilic constituent, some other 'ground substance' of acidophilic properties must be present in them.

*Cytoplasm.*

In the young lymphocystis cells the lighter portion of the cytoplasm has the regular shape of a sphere slightly invaginated by the nucleus (Pl. II, fig. 7). At the time when it is about to start its rapid development, the inclusion body is found situated at the periphery of this sphere, and often on the opposite side to the nucleus. Later on, when it assumes the form of a calotte, it expands in close contact with the 'sphere'. When the inclusion body is seen growing symmetrically around the nucleus the lighter staining cytoplasm may also encircle the nucleus, thus interposing itself between the inclusion body and the nucleus. The frequent deviations from the regular course of development of the inclusion bodies, mentioned above, show their effects on the 'spheres' also, as the latter may be pierced by the growing bars or divided into fragments.

The interpretation of the succeeding sequence of events is uncertain. For when the inclusion body passes through the transitory stage mentioned above, characterized by its irregular growth, the cytoplasm exhibits darker and lighter patches and, moreover, develops a more distinctly reticulated texture. With further growth the reticulum becomes gradually less distinct, while the areas of differently stained cytoplasm merge together into larger patches giving to the cell a chequered appearance (Pl. II, figs. 12, 13). At this time there is also noticeable a certain change in the chemical reaction of the cytoplasm, for it now stains better with the cytoplasmic dyes, whereas in the former stages it showed basophilic tendencies.

The variegated picture of this transitory stage of the lymphocystis cells may be looked upon as reflecting the major disturbances caused by the disproportionately quick growth of the virus substance; the more regular arrangement of various cell constituents in the later stages gives the impression that some equilibrium is being restored among them. Thus, when the inclusion network reaches the stage at which it assumes the form of a more regular basketwork expanding towards the periphery of the cell, the two kinds of cytoplasm begin to accumulate, one in the centre of the cell and the other nearer to the periphery. This process leads to the formation in cells of *c.* 150 $\mu$ and upwards, of a cortical ectoplasmic layer, of more homogeneous structure, and more coarsely granulated endoplasm (Pl. II, figs. 12, 13).

The difference in staining properties of the ectoplasm and endoplasm may not be seen equally well in all cells, but, in many of them, the cortical layer appears sharply delimited, exactly as in Joseph's photomicrographs. Thus, in this differentiation of the cytoplasm also, the lymphocystis cells in *Mullus surmuletus* exhibit a great resemblance to those of *Sargus annularis*.

The different appearance of the ectoplasm in which the inclusion networks are situated must obviously reflect its particular properties; the difference in the behaviour of the two cytoplasmic layers is occasionally made evident in some degenerating cells in which the ectoplasm with its inclusion bodies is partly folded and detached from the endoplasm (Pl. III, fig. 16).

The question arises: if in the youngest cells two kinds of distinctly different cytoplasm are present, could the ectoplasm and endoplasm of the older cells be considered as deriving directly one from the lighter and the other from the darker staining portions? The evidence gained from the examination of the preparations stained with different methods is not unequivocal.

In the sections stained with Azan, or haematoxylin and eosin or xylidin red as counterstain, or even with haematoxylin alone, the 'spheres' in the small cells are always lighter in colour. In the transitory stage the direct observation of their fate is uncertain, but it seems more probable that the lighter stained areas of the cytoplasm derive from these spheres. When the differently stained portions become larger and more distinct the lighter ones are moving towards the cell periphery. Hence it may be concluded that the 'sphere' develops into the ectoplasm of the larger cells (Pl. II, fig. 12).

If, however, the preparations are stained with Giemsa the results are contradictory. In the small cells the spheres stain, as with other dyes, in a markedly lighter hue; in the transitory stage the intensively stained reticular structures of the cell dominate the picture, while other cytoplasmic elements are less recognizable; in the later stages the differently stained patches of the cytoplasm become apparent and even show more details of the distribution of the two kinds of the cytoplasm, but in this case the darker staining parts are moving towards the periphery (Pl. II, fig. 13). This phenomenon casts doubt on the former assumption which, moreover, does not agree with Joseph's statement that the endoplasm derives from the sphere. The problem must therefore remain unsettled.

### *Nucleus*

The nucleus, which is very large in the young cells, grows more slowly than the cell itself, so that its volume, in proportion to that of the cell, becomes smaller with the progressing hypertrophy of the latter. It occupies a position at the periphery of the cell, where it is situated immediately under the cell membrane. In the larger cells the original globular form may undergo some modification, becoming ellipsoidal or invaginated, but these alterations do not distort the spherical outlines of the nucleus to such a degree as described by Joseph, and in this respect the lymphocystis cells in *Mullus* appear to differ to a greater degree from those in *Sargus*.

The constitution of the nucleus has a great similarity in both these species. It is characterized by the abundance of the nuclear sap, a very fine and sparse framework, and a large nucleolus. The latter shows great variability in form; it may include vacuolar spaces, become fenestrated, or develop irregular lobes which if detached by deep constrictions are found as separated fragments. Although young cells with two nuclei may sometimes be observed, this fragmentation of the nuclear mass seems to be chiefly responsible for the occurrence of more than one nucleolus in the larger cells.

## ABNORMAL FEATURES IN THE LYMPHOCYSTIS CELLS

### *Binucleated Cells*

Cells with two nuclei are not infrequently met with in younger stages. In the group of small cells, shown in Pl. II, fig. 5, two such cells are present. Both nuclei have an identical structure, and there is certainly no question of one of them belonging to the category of elements described by Nigrelli & Smith. Larger cells with two nuclei were observed in a few instances only. This rare occurrence may be partly due, as the cells grow larger, to the decreasing chances of meeting both nuclei cut in one section at a suitable angle. It is also possible that the course of development of some of these cells is unusual. An interesting example is seen in Pl. II, fig. 12 (middle right), in which a binucleated cell contains two inclusion bodies in the calotte stage, occupying diametrically opposed positions with the sphere-cytoplasm between them and the nuclei. Further development in this direction may perhaps account for the Siamese-twin monstrosity represented in Pl. III, fig. 14.

### *Several Cells in One Membrane*

Pl. III, fig. 15, shows seven cells, two of them very small, encircled by one collapsed membrane which obviously belonged to a large degenerated cell. In this section only part of the cells included in this way can be seen, and on looking through the following sections it was found that there were fifteen in all. Such cases cannot be very uncommon, as in a second tumour a group of six cells was found similarly enclosed in a membrane. There can hardly be any doubt about the process of formation of such features, in view of the fact that the large cells in their degenerating state (which will be discussed below) are often invaded by the connective tissue elements. If now among the latter there happen to be some carrying the virus infection they must start their development into the lymphocystis cells within the membrane of the old cell, and it may be stated that, in this as in other instances, the membrane can persist a long time after all other cell elements become completely resorbed.

## DEGENERATION OF THE LYMPHOCYSTIS CELLS

Of all previous writers, Joseph paid most attention to the processes of degeneration of the lymphocystis cells. His findings may be summarized as follows: (i) the degeneration affects exclusively the large cells which have reached the peak of development; (ii) degeneration may proceed in two ways: either the membrane of the cell becomes ruptured at some point and the elements of the surrounding connective tissue penetrate into the lymphocystis cell, or the degeneration proceeds without this perforation of the membrane; (iii) if the cells in the process of degeneration are situated near to the epidermis the latter becomes stimulated and produces buds which extend into the adjacent tissue, filling up the spaces left by the shrinking lymphocystis cells.

The first of these statements certainly does not apply to the lymphocystis cells in the red mullet, for, as has been mentioned, the process of degeneration may be observed in cells in various stages of development. As to the third point, i.e. the part played by the epidermis, nothing of this kind could be seen: the epithelium tissue is everywhere sharply delimited and does not show any tendency to grow towards the connective tissue. However, the small amount of material which I had for investigation was insufficient to enable me to conclude with certainty that no such stimulation of the epidermis would ever occur in *Mullus* tumours.

The remaining statements by Joseph, concerning the two processes of degeneration, could be fully confirmed and, owing to the abundance of the degenerating cells in the tumours of *Mullus*, various stages of their disintegration could be observed even on the same section. Sure symptoms of this process, which are more noticeable than the above-mentioned changes in the appearance of the inclusion bodies, are the irregularities of the outline of the nucleus and of the cell itself. If the membrane is ruptured it soon becomes invaginated in various ways, assuming bizarre outlines in the sections. At the same time, small cells from the surrounding connective tissue invade the opening and contribute to the disintegration of the cell contents. When the membrane remains unperforated it may also exhibit certain deformations while the cell undergoes a gradual resorption, but degenerating cells may often be seen in which the dwindling cytoplasm becomes detached from the membrane and the latter preserves for a long time its spherical outlines. In Pl. III, fig. 17, which shows many cells in different stages of degeneration in which the membranes are selectively stained, there may be seen: (*a*) empty membranes; (*b*) membranes with numerous small infiltrating cells; and (*c*) some in which the shrinking cytoplasm has become retracted from the membrane.

In the larger cells both kinds of degeneration, viz. with and without rupture of the membrane, occur. In those of medium size and in smaller ones the membrane shows more resistance, and the resorption of the cell contents goes on without its perforation.

The course of the degeneration process, the changes in the appearance of the cytoplasm, and the disintegration of the nucleus and of the inclusion bodies, can easily be followed in their various stages, and it can be said that Joseph's description of *Sargus annularis* would apply equally well for *Mullus surmuletus*. It should be added, however, that in the latter not all degenerating cells follow the same course, for there is yet another kind of change which some of the lymphocystis cells may undergo; this is characterized by a peculiar activity of the inclusion bodies, in which there is a series of transformations now to be described.

## TRANSFORMATIONS OF THE INCLUSION BODIES IN THE DEGENERATING CELLS

As has been mentioned above, the inclusions of the largest cells may show some modifications in their structure, which have been interpreted as being of a regressive nature, indicating the beginning of the disintegration of these bodies. This assumption seems to be justified, since many intermediate stages have been observed between the typical appearance of the inclusions in medium-sized 'healthy' cells (Pl. IV, fig. 20) and in the degenerating cells (Pl. IV, fig. 21). The process by which these changes are brought about may be compared to a slow melting. At first the outlines of the networks become slightly modified; later on the progressive dissolution of finer linking bars leads to the breaking off of fragments of different sizes, whose finer structure gradually becomes indistinguishable. Finally, the network is reduced to a number of irregularly shaped globular fragments, dwindling in size and number until they disappear altogether.

In some of the degenerating cells of the medium-sized group in which the membrane does not become perforated quite a different process occurs. Not only does the inclusion network not show any signs of this dissolution process, but it starts to grow, developing at the same time a more finely detailed structure. The first recognizable stage may be seen in Pl. IV, fig. 22. In the cell on the right the bars of the inclusions, compared with those of the cell on the left, are beginning to grow a little thicker, and some changes in their fine structure become noticeable. Further transformations in the same direction lead to the appearance shown in Pl. IV, fig. 23, which is markedly different from that in Pl. IV, fig. 20. Even if such 'normal' inclusion networks may sometimes exhibit a more delicate structure than seen in this figure (fig. 20), they always show the same characteristic pattern of alveolar spaces within the bars; whereas in the stage of transformations shown in Pl. IV, fig. 23, the network resembles rather a tridimensional lattice the spaces of which are more or less losing their rounded outlines. Moreover, this lattice does not grow symmetrically; parts of it may become elongated in one direction to form strands of various shapes, sometimes even arranged in lamellae (Pl. IV, fig. 24). If such strands are cut transversely the cross-sections of finer threads might be taken at first sight for separate small bodies (Pl. IV, fig. 25).

Such pictures of networks whose lattice-like structure may be fairly distinguishable on the photomicrographs are comparatively rare; more often the dense and deeply stained networks give a blurred image (Pl. IV, fig. 26).

Whether in the course of this process more inclusion material is produced, or whether that already present at the beginning of the transformations merely becomes rearranged in such a way that its dimensions are increased, is difficult to determine. Anyhow, the inclusions gradually occupy larger areas in the cells, the spreading thread-like bars of the lattice penetrating the cytoplasm so that in the sections the meshes of the inclusions are seen to enclose the cytoplasmic substance.

At a certain stage the network apparently acquires some new property and begins to exert a lytic action on the cytoplasm. At first small spaces appear around the threads of the network, but soon the cytoplasm enclosed in its meshes breaks up into lumps, which disintegrate in their turn into smaller particles. In consequence of this process larger spaces are formed, filled with the framework of the inclusion bodies and particles of the cytoplasm (Pl. IV, figs. 27–29). As these spaces reproduce the pattern of the growing inclusions they represent a system of irregular canals, some of them ending blindly, others joining to form larger lacunae which assume various shapes in the sections (Pl. IV, figs. 30, 31).

Up to a certain stage of these transformations the inclusion network in the lacunae stains very well. Then, however, a change occurs in its elements, causing them to appear fewer in number, until, finally, they become invisible. Whether the networks are dissolved into submicroscopic particles, or whether their chemical reaction becomes changed, could not be ascertained, since the lacunae are filled with a debris of disintegrated cytoplasm. Without differential staining discrimination of the fine fragments of the inclusions, were they really present, is therefore hardly possible. Whatever may be the true nature of this change it must come about in a comparatively short time, since few cells in transitional stages occur; and there may also be seen, not uncommonly in the same cell, some of the lacunae containing a distinctly stained basophilic network, and others in which it is already disappearing. In Pl. IV, figs. 28–31, are shown cells with inclusions in various stages of this process. The differences in the staining reaction cannot be well rendered in the photographic reproduction, and only parts of the network actually present in the preparations can be focused, but in the original sections stained with contrasting nuclear and plasmatic stains the following contents of the lacunae could be well distinguished. In Pl. IV, fig. 28, there shows a very delicate basophilic network, which later, as seen in Pl. IV, fig. 29, becomes markedly reduced (the large lumps are fragments of the cytoplasm); in Pl. IV, fig. 30, at *a*, are intensely stained basophil elements; at *b* fine basophil threads similar to those in Pl. IV, fig. 29, and at *c*, no basophil elements at all. In Pl. IV, fig. 31, only a very few particles show affinity to chromatin dyes, and practically the whole contents of the lacunae stained the same colour as the surrounding cytoplasm.

As regards the behaviour of other elements of the cells in which all these transformations are taking place it should be noted that often the differences in the appearance of the two protoplasmatic layers, i.e. the ectoplasm and the endoplasm, become more accentuated at the time of formation of the lacunae and, moreover, the territory of the ectoplasm in which the lacunae are situated becomes enlarged at the expense of the receding endoplasm (Pl. IV, fig. 31). It seems, therefore, that the substance which becomes destroyed by the inclusion bodies must be of ectoplasmic nature, but this cannot be an invariable rule, for at some places the lytic process is seen to encroach on the endoplasm also.

It may be mentioned that the ectoplasm of the cells in which the transformations take place stains more deeply than that of other lymphocystis cells. Only after the stage has been reached at which the basophil substance disappears, and even then presumably not until some further time has elapsed, do the cells lose this property and take on a distinctly lighter tone.

In some of the cells a remarkable increase of the nucleolar substance could be noticed (Pl. IV, figs. 27, 30). As, however, the nucleoli in the lymphocystis cells of *Mullus* may be of different sizes and shapes, it cannot be said for certain whether such increase in volume is a constant feature of the cells having inclusions in process of transformation.

As seen in Pl. IV, fig. 31, very large areas of the cells may be occupied by the widening lacunae, but no cells were found whose whole territory was invaded in this way. It appears, therefore, that the destructive action of the inclusion network comes to an end with the vanishing of the basophilic reaction.

In further stages the number of particles enclosed in the lacunae is diminishing, and finally many of the lacunae appear as empty or nearly empty spaces. At the same time progressive degeneration leads to distortion of the outlines of the cells and the resorption of their contents.

It is tempting to suggest that all these modifications of the inclusions have a particular significance in the life cycle of the virus of the lymphocystis disease, and that they may presumably be regarded as preparatory stages in the transformation of the virus substance into a state in which it is ready to infect new cells of the same host or of other specimens. The rearrangements of the inclusions into a more delicate network may be regarded as transition stages of the dissolution of the compact aggregations of the virus into particles of submicroscopic dimensions. It is interesting to note that transformations of the virus substance are evidently not confined to simple disintegration since, as we have seen, the relations of the virus to the host cells enter a new phase manifested by the lytic action on the cytoplasm of these cells.

Whether the disappearance of the basophilic reaction should be ascribed only to the disintegration of the virus agglomerations into submicroscopic particles, or be due to some chemical changes, is a question to which no definite answer can as yet be given.

The fact that the majority of the lymphocystis cells degenerate without showing any activity of their inclusions leads to the assumption that the transformations may find the right conditions to start in comparatively few of the cells. Indeed, in the tumours investigated only one group of such elements has been found. It appears that even when these transformations are in progress they are liable to be interrupted at any stage. Then the inclusion bodies, instead of increasing still further in size and developing a more delicate structure, show reverse changes turning into uniformly stained bodies of rounded outlines. Their origin from those inclusions which have started their transformations may be recognized by their dimensions, and the differences in these dimensions indicate the moment at which the process of the transformations was stopped and switched into a degenerative one (Pl. III, figs. 18, 19).

If we take the above interpretation of the behaviour of the inclusion bodies for granted, we have to assume that the completion of the life cycle of the infective agent can only be achieved in a few of the growing lymphocystis cells and apparently only in some of those which have not reached their maximal dimensions; in all others it would meet its doom. The degeneration which overcomes the virus substance during its transformations, as well as all similar processes observed in the lymphocystis tumours, are evidently manifestations of the struggle of the host organism with the infection. A similar struggle must certainly occur in other diseases in which the infective agent is localized in certain cells, and the organism attacked is capable of mobilizing its defensive measures. A remarkable feature of the lymphocystis disease is that, owing to the unusual dimensions of the affected cells and the staining properties of the virus agglomerations, it affords illustrations of the various stages of this struggle.

The importance of certain transformations as essential links in the life cycle of the virus can be related to the periodicity of eruption of new tumours, which could be explained by assuming that the transformations take place at certain times and in relatively few cells only. This would tally with the occurrence of the earliest stages of the infected cells and of the transformations in the same specimen of *Mullus surmuletus*. It would agree also with the view expressed by Weissenberg (1945) that some changes in the lymphocystis virus agglomerations might possibly take place before it is ready to produce new infections.

On the other hand, although the evidence favours the above suggestion, it may be open to dispute on the grounds that similar transformations of the inclusions were not observed by those investigators who made detailed researches with much more abundant material. In the paper of Joseph illustrated by as many as ninety photomicrographs, only one (fig. 43) shows an inclusion body with a swollen appearance somewhat similar to one of the stages I have described. No reference is, however, made to this figure in the text. Further, if such transformations had not been noticed in the lymphocystis cells of *Acerina cernua* or *Stizostedion vitreum* and, nevertheless, Weissenberg's infection experiments with the same material were successful, this would tend to discount their alleged importance. Unless, therefore, one assumes that the transformation of the inclusions did not, owing to their rare occurrence, chance to turn up in the preparations from other fishes, some doubts may legitimately arise as to the interpretation of the phenomena observed in the red mullet. It is desirable, therefore, that particular attention should be given to this point in the future.

I wish to record my gratitude to Mr G. A. Steven for the material which has been worked out in the present paper. Thanks to his observation of the unusual outgrowths, and the suggestion that they would be worth examination, the number of species known to be affected by the lymphocystis disease has been increased by the addition of *Mullus surmuletus*.

I am also greatly indebted to Mr F. S. Russell, F.R.S., for his kind help in preparing the manuscript.

## SUMMARY

A case of lymphocystis disease is described in the red mullet (*Mullus surmuletus*) from Plymouth waters. The tumours produced by this disease showed typical lymphocystis cells in all stages of development up to 430 $\mu$ in diameter. Apart from minor differences the organization of the cells closely resembled that described by Joseph in *Sargus annularis*; this was especially so as regards the so-called inclusion body, a basophil staining network situated in the cytoplasm and probably representing the agglomeration of the virus agent of the disease.

The development of the lymphocystis cells which originate from the fibroblasts was observed in its earliest stages. The inclusion bodies appear in the young cells as several (up to five) granules which most probably soon merge into larger bodies. They have the characteristic appearance greatly resembling the Guarnieri bodies, as do those discovered by Weissenberg in lymphocystis cells of *Acerina cernua* and other species. Their further development follows the same lines as observed by other writers. There is no evidence in favour of the idea that the inclusion bodies may be derived from the nuclear matter of the cell.

Various forms of the degeneration of the lymphocystis cells have been observed. Special attention has been given to the activity of the inclusion bodies in certain types of degenerating cells. This is characterized by the swelling of these bodies and the rebuilding of their substance into a network exhibiting much more delicate structure and exerting a lytic action on the cytoplasm of the host cell. As these transformations progress the network becomes less distinguishable in the lacunae formed in the cells by the disintegration of the cytoplasm, until finally its elements, previously staining distinctly with chromatin dyes, cannot be discerned any more.

It is suggested that these transformations may represent those stages in the life cycle of the virus agent during which it acquires the ability to transmit the infection to other cells of the same host or other specimens.

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## EXPLANATION OF PLATES

All photomicrographs have been made from preparations of the lymphocystis tumours of *Mullus surmuletus*. The material was fixed in Bouin's fluid and embedded in paraffin. The preparations represented in figs. 1–12 and 17–31 have been stained with Weigert's iron haematoxylin and various counterstains, those in figs. 13–16 with Giemsa's stain.

### PLATE I

Fig. 1. Part of a lymphocystis tumour with cells in various stages of development and degeneration. The large upper portion composed of cells of nearly equal size has presumably originated at a later eruption of the disease than the remaining portion of the tumour. The degenerating elements are seen also in the middle of this younger portion.

Fig. 2. Part of the lymphocystis tumour covered by cutaneous epithelium.

Fig. 3. Group of the youngest lymphocystis cells among others advanced in their development. Note in the latter the aspect of the inclusion network cut at various angles.

Fig. 4. Group of lymphocystis cells older than those in the preceding figure with various stages of development of the inclusion bodies. Other cells greatly hypertrophied. Note the shape of the nucleolus in the large cell.

### PLATE II

Figs. 5–11. Early stages of the lymphocystis cells. All photographs have the same magnification. Fig. 5: *a*, connective tissue cell showing changes most probably representing the first stages of the evolution of the lymphocystis cells; *b*, cell with five basophil granules (not well distinguishable on the photograph); *c*, cell with a 'sphere'; *d*, binucleated cells; *e*, cells with inclusions in the Guarnieri-body stage. Fig. 6: *a*, small cell with distinct characters of lymphocystis element; *bl*, blood vessel with an erythrocyte. Fig. 7: cells with distinct spheres and inclusion bodies. Fig. 8: cells with inclusion bodies of various sizes; the largest with two bodies which are going to fuse. Fig. 9: further stage of the merging of two inclusion bodies. Fig. 10: cell with three inclusions, one of them as well as the big inclusion in the second cell seemingly representing the final stage of the fusion of two granules. Fig. 11: cell with two inclusions; the larger has a lobed appearance probably caused by the outlines of three granules fusing into one.

Fig. 12. Several cells with lighter and darker portions of the cytoplasm irregularly distributed and becoming arranged, in the larger cells, as ectoplasm and endoplasm. Note on the right side of the figure a small binucleated cell with two 'spheres' and symmetrically developing inclusion bodies. Haematoxylin-eosin staining.

Fig. 13. Cells in the same stages as in the preceding figure but stained with Giemsa's. The darker staining cytoplasm assembles on the periphery of the cells. Note the distinctly delimited ectoplasm in the large cells.

### PLATE III

Fig. 14. Two cells united by a cytoplasmic bridge.

Fig. 15. Several cells developing within the membrane of a degenerating cell. Other cells in this and the preceding figure are in various stages of the degeneration.

Fig. 16. Part of the lymphocystis tumour in which nearly all cells have degenerated. *a*, empty membranes; *b*, membrane with invading connective tissue elements; *c*, membrane with shrinking cell contents.

Fig. 17. Degenerating cell in which the ectoplasm containing the inclusion bodies is partly folded and detached from the endoplasm.

Figs. 18, 19. Inclusions of different appearances depending on the stage of their development interrupted by the degeneration. Fig. 18: *a*, degenerating inclusions which have not started their transformations; *b*, those which were in the early and (fig. 19) in the later stage of transformation.

### PLATE IV

All photomicrographs have been made with the same magnification (oil-immersion $\frac{1}{7}$ in.).

Fig. 20. Usual 'normal' appearance of the inclusion bodies on a tangential section of a lymphocystis cell of medium size.

Fig. 21. Disintegration of the inclusion bodies in cells degenerating in the manner observed in the majority of the lymphocystic cells.

Fig. 22. First signs of transformations of the inclusion bodies seen in the cell on the right. Note the swelling of the bars and their more delicate structure as compared with the cell on the left.

Fig. 23. Rearrangement of the inclusion networks in a lattice made up of delicate threads.

Fig. 24. Arrangement of the transformed network in strands and lamellae.

Fig. 25. Similar stage as in preceding figure with several strands cut transversely.

Fig. 26. Part of a lymphocystis cell with inclusions in a transformation stage slightly older than in fig. 22, showing increasing area occupied by these bodies. In order to make the inclusions more prominent a red filter was used and therefore in figs. 20–26 the cytoplasm in which the networks are developing is rendered nearly invisible.

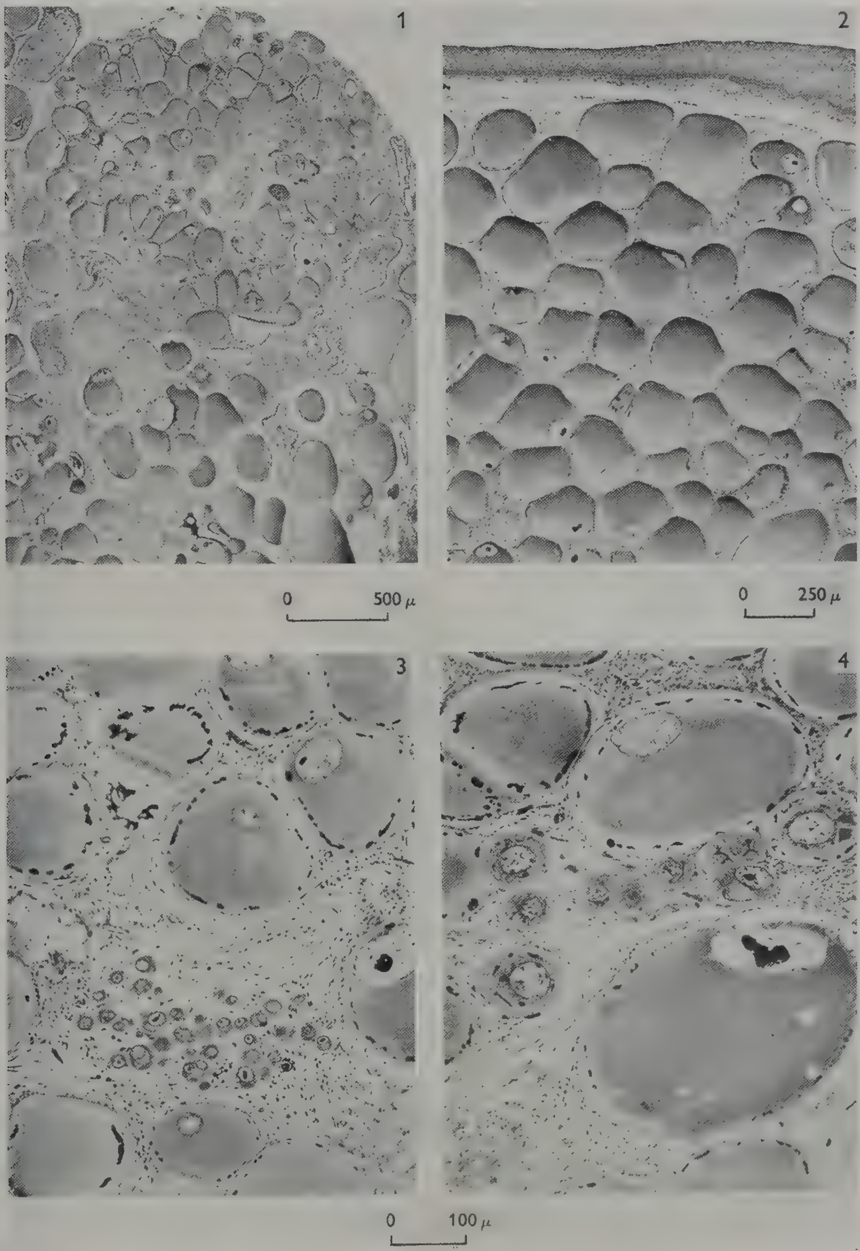
Fig. 27. Part of a lymphocystis cell with the first stages of the dissolution of the cytoplasm. *a*, cross-sections of thicker and very thin threads of the network with narrow spaces around them indicating the beginning of the dissolution seen in more advanced stages round the larger parts of the inclusions; *b*, inclusion network flattened in lamellae which, being forshortened in the picture, do not show their finer structure; *n*, degenerating nucleus with large masses of nucleolar origin.

Fig. 28. Lacunae with fine threads of the inclusion network.

Fig. 29. Lacunae with lumps of disintegrated cytoplasm and threads of inclusion network in the stage when they are becoming less visible.

Fig. 30. Parts of three lymphocystis cells with lacunae containing in *a*, deep stained basophil elements; in *b*, lumps of cytoplasm and hardly visible basophil threads; in *c*, particles of various sizes not giving any basophil reaction. Note the shapes of the lacunae cut at various angles and the large nucleolar mass in one of the cells.

Fig. 31. Lymphocystis cell in an advanced stage of the formation of the lacunae filled up with particles not showing basophilic staining reaction. Some of the lacunae are empty. Note the enlarged territory of the ectoplasmic layer.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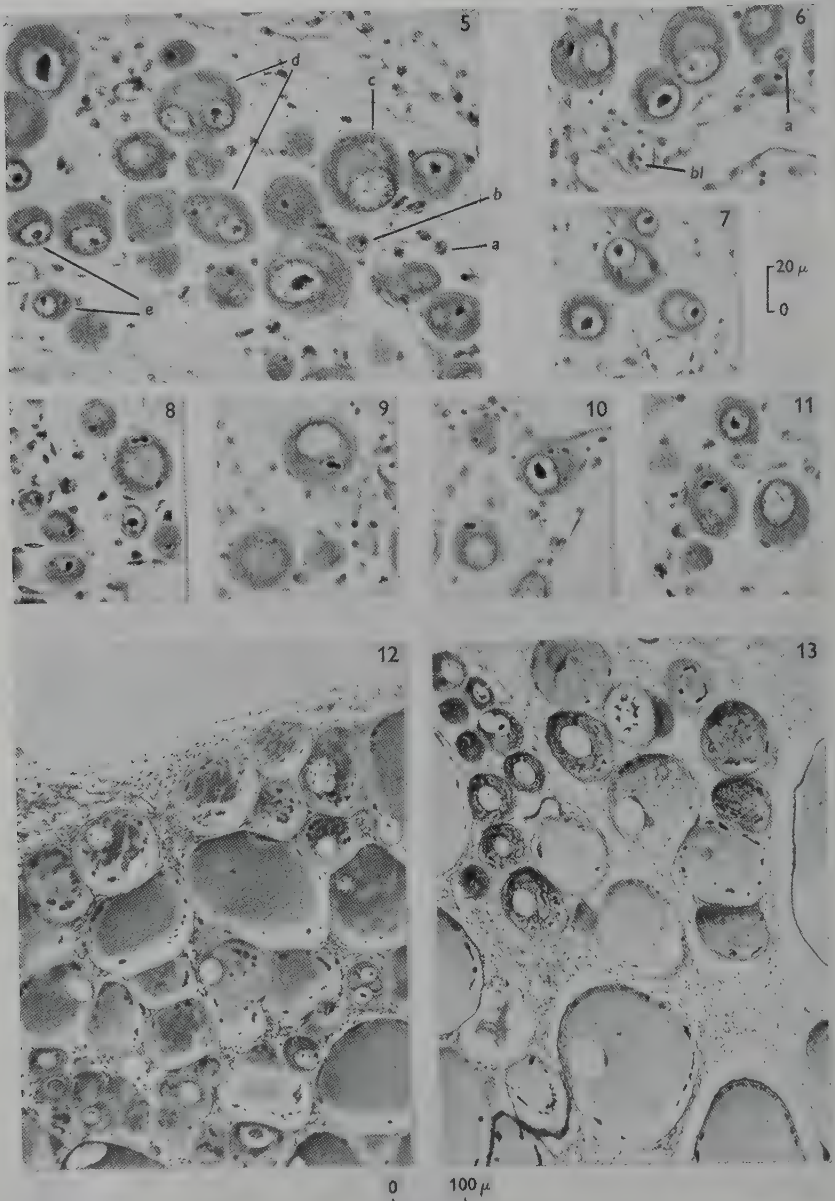
Figs. 1–4.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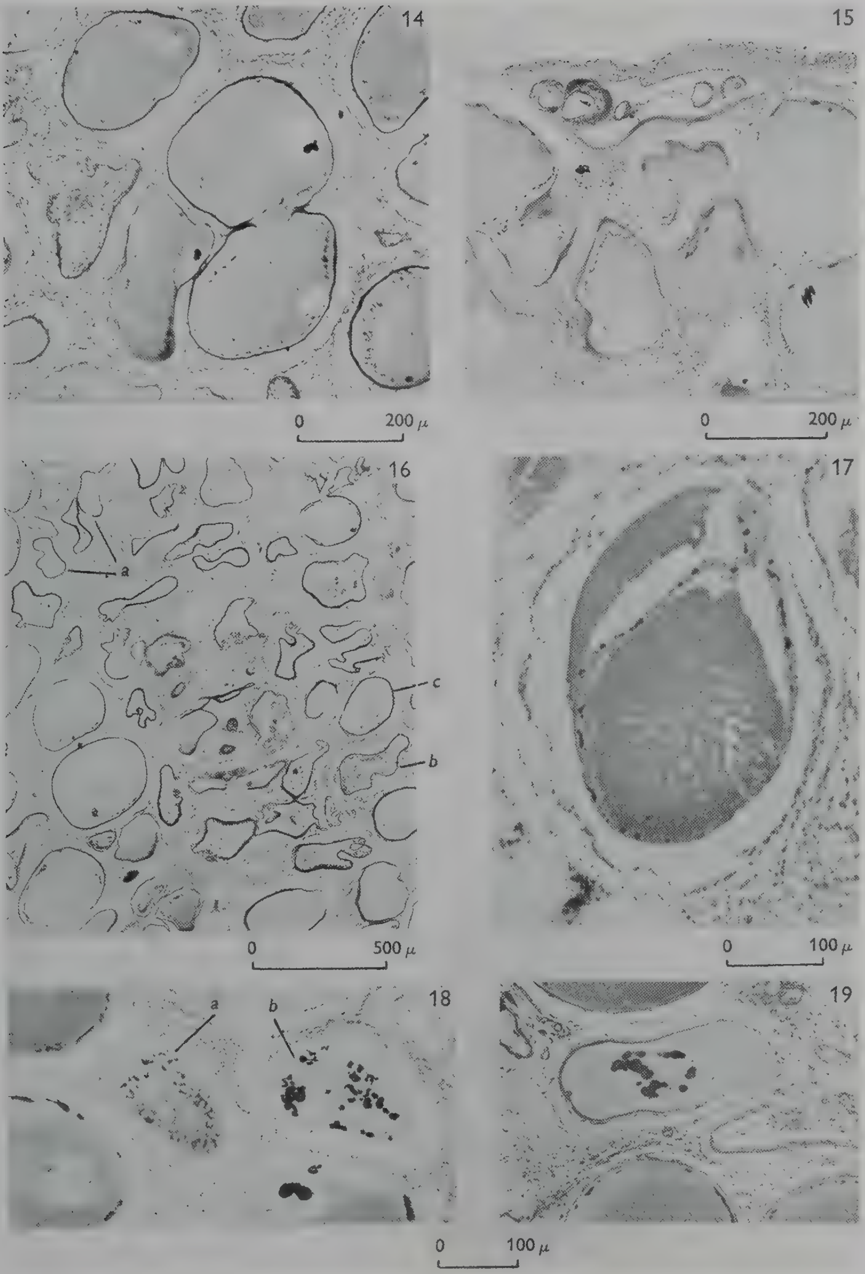
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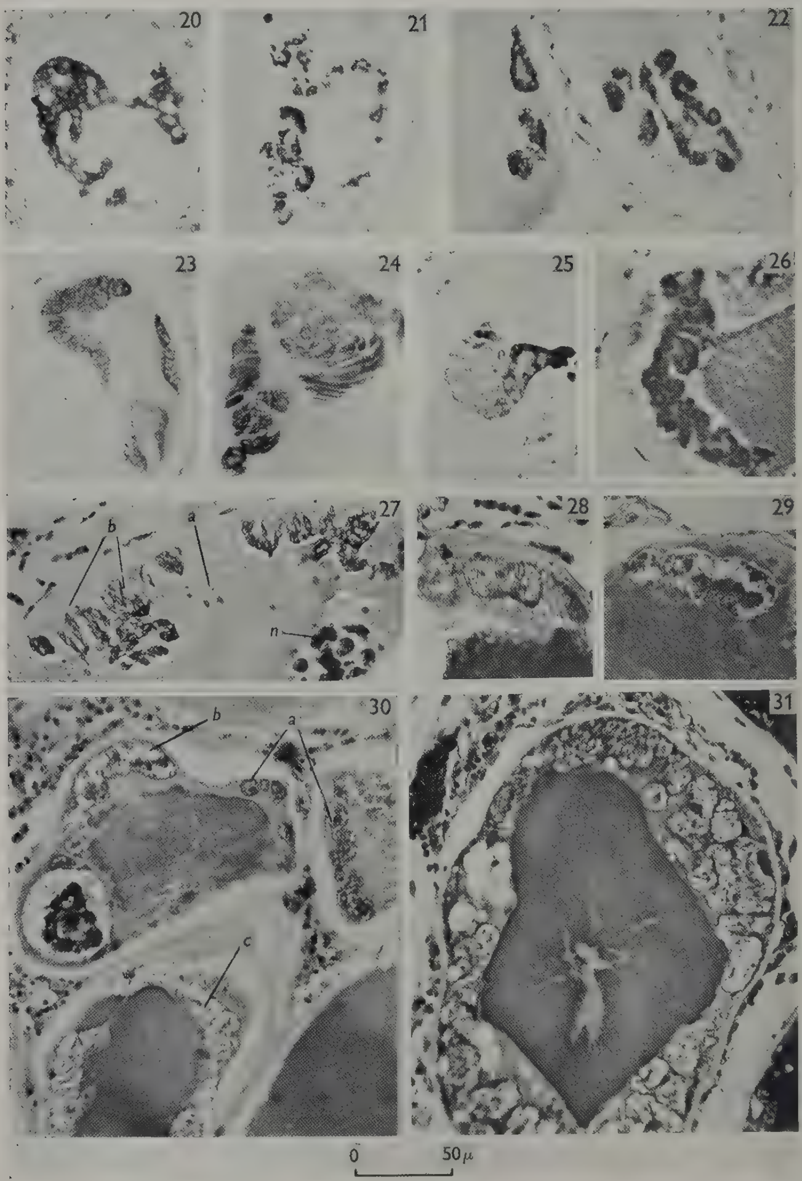
Figs. 14–19.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Figs. 20–31.

# THE BIOLOGY OF THE COMMON PRAWN, *LEANDER SERRATUS* PENNANT

By G. R. Forster, B.Sc.
From the Plymouth Laboratory

(Text-figs. 1–14)

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## INTRODUCTION

This work was undertaken at the suggestion of Mr F. S. Russell that little was known about the natural history of even so familiar a species as *Leander serratus*, the common prawn of the English Channel, which may at times form a valuable natural resource to the inshore fishermen. Attention was therefore chiefly concentrated on its growth rate and breeding biology. In spite of the long breeding season the statistical method of studying growth was adopted when preliminary results appeared successful. By this method additional data could be obtained on distribution and migration. In the closely related genus *Crangon*, growth has been shown to be retarded under laboratory conditions (Nouvel & van Rysselberge, 1937), so that an experimental study could not be relied on to give a picture of the normal life history. Höglund's recent monograph (1943) has treated *Leander squilla* in great detail. However, this species differs considerably in size and distribution from *L. serratus*, and it was felt that a similar study in the Plymouth area would not be mere repetition; in fact the biology of *L. squilla* itself differs somewhat in the two districts.

Acknowledgement is due to the Department of Scientific and Industrial Research for financial assistance in the form of a maintenance allowance, and to the crews of the research ships of the Plymouth laboratory for their help in collecting. Mr W. Searle's experience of the Plymouth trawl fishery for prawns also proved a great benefit.

## METHODS

Prawns were caught by three methods: trawling, hand-netting, and with baited traps or hoop-nets.

The trawl used from the motor boat *Gammarus* was identical with the commercial prawn trawls, consisting of a 6 ft. beam with 1 in. mesh netting on the wings and head and $\frac{3}{4}$ in. mesh in the cod end. Trawling grounds near Plymouth are described in the *Plymouth Marine Fauna* (Marine Biological Association, 1931). The best grounds are located chiefly in muddy areas, sometimes a little rough, or near rocks.

Several patterns of hand-net were used, a pear-shaped frame for rock pools and a rectangular frame for walls or pier piles. Half-inch mesh netting was found suitable for all except the youngest stages, for which stramin was necessary. The most successful places for hand-netting were pier piles and undercut rocky gullies or crevices where the larger brown algae were absent.

Twelve prawn traps were constructed in the form of miniature lobster pots 2 ft. × 1 ft. × 8 in. covered with $\frac{1}{2}$ in. mesh netting. They were laid overnight in fleets of four, baited with fish. Catches varied considerably from trap to trap, usually one out of the four being particularly successful. The largest catch from any one trap was 37 prawns. At Paignton, additional catches were made with hoop-nets kindly loaned by Mr S. Underhay. These nets were set after dark in the *Laminaria* zone and hauled at about quarter-hourly intervals, the technique being to raise the net slowly and gently at first, when the prawns remain clinging to the bait. If the net is given a sharp tug some are disturbed and escape.

Prawns were always measured in fresh condition, owing to the curvature of the abdomen in most preserved specimens. In all cases the total length (tip of the rostrum to base of the spines on the telson) was measured with dividers while the animal rested in its normal upright position on a glass plate. Living prawns could be induced to sit quietly in this position. Although an occasional specimen was taken with a damaged telson or rostrum, with practice it was easy to estimate the extra few millimetres accurately. This method has the advantage of being suitable for all sizes of prawns. Variations in the rostral length, though tending to increase the spread of the results, did not hinder the separation of different year groups. Measurement of the carapace length alone, though suitable for adults, was virtually impossible for juveniles, and had two further possible disadvantages. An error of ½ mm. is much greater relative to the carapace than to the total length. Secondly, the carapace might undergo heterogonic growth while the ovary is ripening.

Collections were started in October 1949 and the observations continued until October 1950.

## AGE AND GROWTH

### *The* 1950 *O-Group* (*i.e. Brood of the Year*)

Juvenile and post-larval stages belonging to the 1950 O-group of *Leander serratus* were first taken from shore pools at Wembury in the second week of July of that year. They had not been found during the previous spring tides at the end of June, and therefore it is unlikely that many arrived before the first week of July. Very small prawns also appeared in the Sound at about the same time, their size frequencies being shown in Fig. 1. The Wembury catch

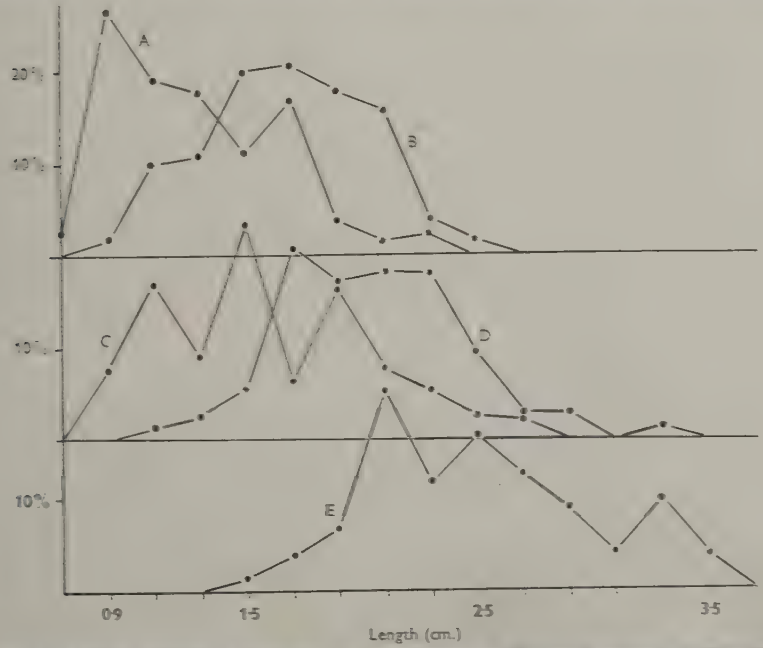

Fig. 1. *Leander serratus*. Percentage size distribution of O-group prawns. A, Rum Bay (Plymouth Sound), 24 July 1950 (136). B, Wembury (outside Sound), 14 July 1950 (127). C, Rum Bay (pool at mid-tide level), 3 Aug. 1950 (77). D, Rum Bay (low-water springs), 3 Aug. 1950 (72). E, Rum Bay (low-water springs), 29 Aug. 1950 (182).

is seen to contain many more prawns in the 1·7, 1·9 and 2·1 cm. groups than those from Rum Bay. At first sight this larger-sized population might be thought to be older or to have grown faster, but catches from Rum Bay on 3 August (Fig. 1) showed that the average size increased towards L.W.S.T. level. Therefore the Wembury catch may have been from a slightly lower level on the shore. The growth of these juvenile prawns is shown in a comparison of the catch of 3 August at L.W.S. with that of 29 August. It is seen that the whole curve has moved roughly 0·5 cm. to the right. There appears to have been only very little further recruitment of small individuals on the left-hand side of the graph.

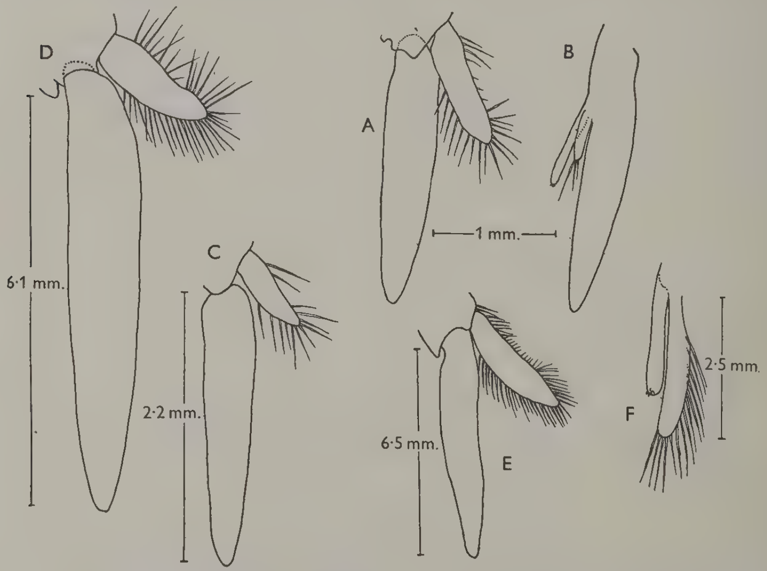

Fig. 2. *Leander serratus*. Secondary sex characters. A, 1st pleopod of immature ♂ (23 mm.). B, setose appendix masculina of the second pleopod of the same. C, 1st pleopod of immature ♀ (24 mm.). D, 1st pleopod of mature ♀ (68 mm.). E, 1st pleopod of mature ♂ (69 mm.). F, appendix masculina of the same. In D and E the inner branch (with setae) has been drawn the same length as in A to show the difference in proportions.

Over a length of 2·5 cm. the males can be distinguished from the females by the shape of the appendix interna of the first pleopod, and by the presence of an appendix masculina on the second pleopod (Fig. 2), these being the normal secondary sex characters. In case some males developed at a slower rate, sexing was not attempted for specimens below 3 cm. in length. This limit had the additional advantages in that it allowed sexing to be done by eye, instead of with a binocular microscope, and also made the stramin net unnecessary since it was difficult for a 3 cm. prawn to escape through the ½ in. mesh of the hand-net.

Collections in September and October 1950 are illustrated in Fig. 3. Growth is shown by the shift of the peak from approximately 3·75 to 4·75 cm. or over. There appears to be no differential growth rate between the sexes up to this stage, although the catch from Burgh Island shows a tendency in this direction. This catch is of interest, since the coast is considerably more exposed to wave action than the Sound. Growth appears to have been just as rapid as in the Sound, but there is a greater proportion of the population in the small-size groups. Possibly in the open sea the chances of the larvae being swept into the littoral zone (where metamorphosis appears to take place) are smaller and therefore the period of settling prolonged.

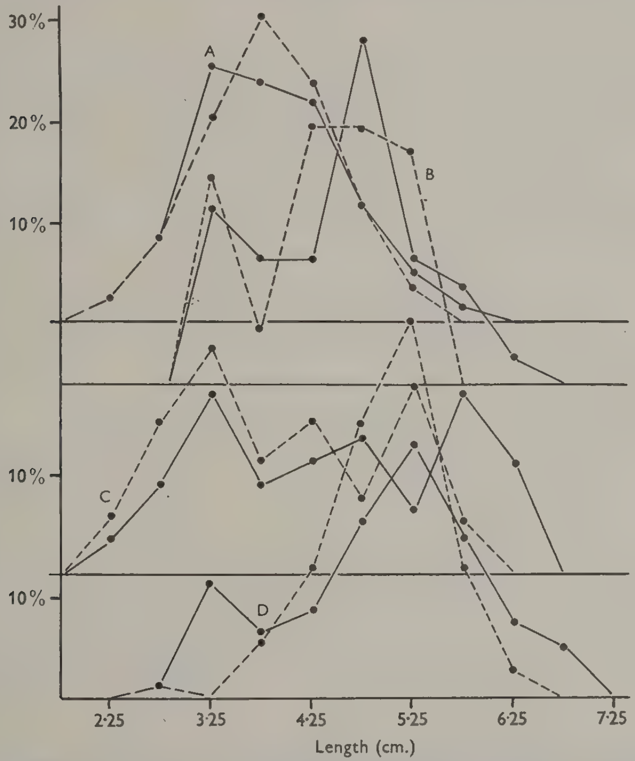

Fig. 3. *Leander serratus.* Length frequencies of the 1950 O-group in the autum. A, Rum Bay, 12 Sept. 1950 (60♀, 60♂). B, Rum Bay, 9 Oct. 1950 (41♀, 39♂). C, Burgh Island (outside Sound), 13 Oct. 1950 (44♀, 27♂). D, Drake's Island, 11 Oct. 1950 (80♀, 70♂). ——, females; – – –, males.

## *Comparison of the* 1949 *and* 1950 *Year Groups*

The overwintering population of prawns was studied from October 1949 onwards. It was therefore necessary to delimit the 1949 O-group for comparison with that of 1950. This was not difficult for the males (Fig. 5), but as shown in Fig. 4 the females presented a more complex pattern. The first

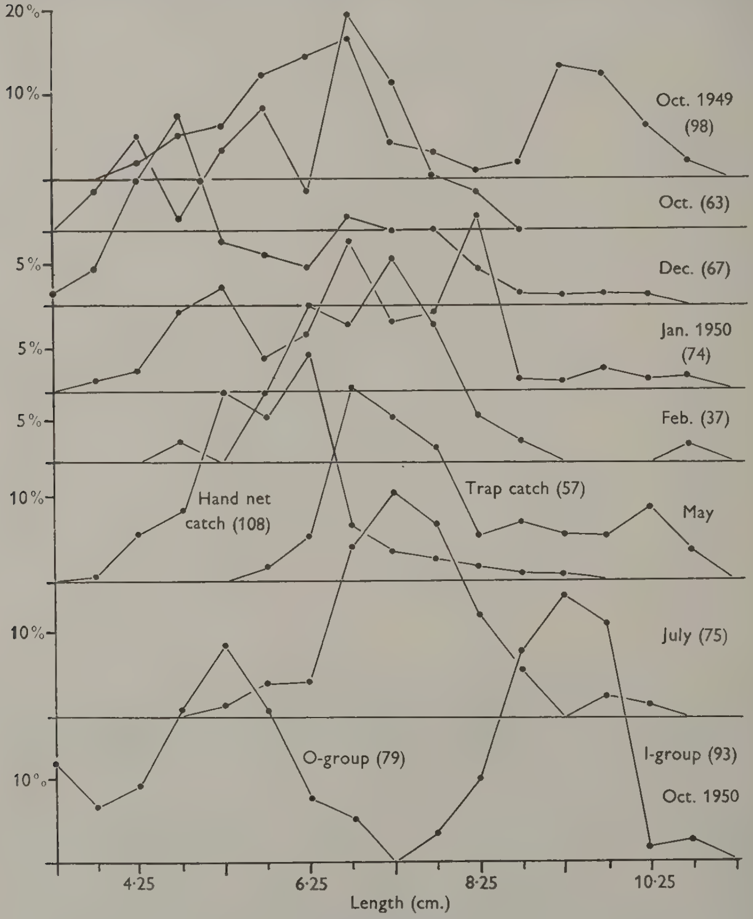

Fig. 4. *Leander serratus.* Length frequencies of selected catches of females, Oct. 1949 to Oct. 1950.

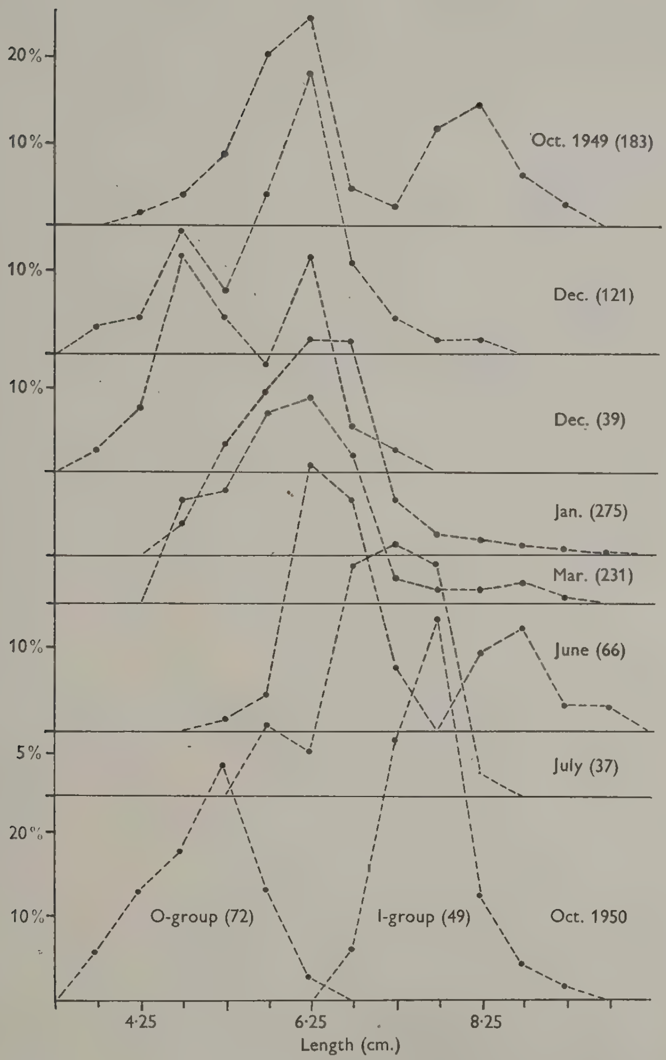

Fig. 5. *Leander serratus*. Length frequencies of selected catches of males, Oct. 1949 to Oct. 1950.

trawl catch (18 October 1949) shows bimodal curves for both sexes, which was a pleasantly simple picture. By December, however, with the males a small secondary peak showed up at 4·75 cm.; while with the females the original peak at 6·25 cm. gave place to a complex pattern with three minor peaks at approximately 4·75, 6·75 and 8·25 cm. This population can only be analysed after a study of catches during the summer of 1950, where it is seen that in 1950 all the prawns from 4·25 to 8·25 cm. groups shift into one peak, which clearly corresponds, although the average length is slightly smaller, to the larger peak at approximately 9·5 cm. in the trawl catch from below the Hoe in October 1949 (Fig. 4). Since the group with the 9·5 cm. peak in October 1950 contains all the smallest prawns before the appearance of the 1950 O-group, it must therefore have been the previous year's brood, i.e. the 1949 year group. By tracing this group back to October 1949, the 1949 O-group can be delimited. It appears to include all males below 7·25 cm. and all females below 7·75 cm. The apparent peak of females at 8·25 cm. in some winter trawl catches is discussed later (p. 342). On this basis, Fig. 6 shows the 1949 and 1950 O-groups superimposed on one another. There is seen to be a

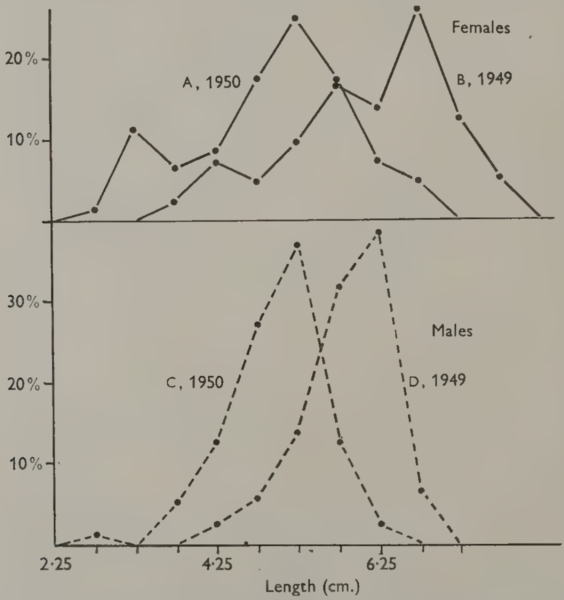

Fig. 6. *Leander serratus*. Comparison of the 1949 and 1950 O-groups in October of the same year. A, Drake's Island, 11 Oct. 1950 (80). B, average of trawls off the Hoe, 21 and 18 Oct. 1949 (60) and Trevol Pier, 20 Oct. 1949 (63). C, Drake's Island, 11 Oct. 1950 (70). D, trawl off the Hoe, 12 Oct. 1949 (116).

difference of about 1 cm. between the peaks for both sexes, the 1949 brood having clearly outgrown the largest October 1950 O-group catch. The year 1949 was exceptional for the warm weather during summer and autumn; whereas 1950 had a much cooler summer. Extraction of the daily sea temperature readings from the bathing station on the Hoe gave the following results. The sea temperature remained above 15° C. for 6 weeks longer in 1949 than in 1950. From 1 July to 12 October inclusive, the average of the daily sea temperature records was 17·27° C. in 1949 and 15·57° C. in 1950. Alternatively, the difference may be expressed as the cumulative (daily) excess temperatures above 15° C., which was 231·8° C. in 1949 and 59·66° C. in 1950.

The problem is therefore to ascertain whether this temperature difference is a reasonable explanation of the difference in mean lengths between the two successive O-groups. Thanks to the assistance of Mr G. M. Spooner, it was possible to calculate the temperature characteristic for growth from the data, and to compare the result with known values.

Assuming that metamorphosis took place at the beginning of July in 1949 and 1950, and that the average length of the post-larva was 9 mm. in both cases, the growth increment (for males only) during the 104 days till 12 October was 49·45 mm. in 1949 and 40·84 mm. in 1950. The average temperatures during this period were 17·27 and 15·57° C. respectively.

The Arrhenius equation for the temperature characteristic $\mu$ is taken from Needham (1931, p. 515):

$$\frac{1}{g_1} \div \frac{1}{g_2} = \exp\left[\tfrac{1}{2}\mu\left(\frac{1}{T_1} - \frac{1}{T_1}\right)\right],$$

where $g_1$ and $g_2$ are the times to reach a definite state at the high and low temperatures $T_1$ and $T_2$ expressed in degrees absolute. In this case the reciprocals of the growth increments during the same period of time are substituted for $g_1$ and $g_2$ (assuming uniform growth for the period).

We then have:

$$\frac{1}{40\cdot84} \div \frac{1}{49\cdot45} = \exp\left[\tfrac{1}{2}\mu\left(\frac{1}{288\cdot57} - \frac{1}{290\cdot27}\right)\right],$$

therefore
$$\frac{49\cdot45}{40\cdot84} = \exp\left[\tfrac{1}{2}\mu(0\cdot000020)\right],$$
$$= \exp\left[\mu \times 10^{-5}\right],$$

therefore
$$\log\left(\frac{49\cdot45}{40\cdot84}\right) = \mu \times \frac{10^{-5}}{2\cdot303},$$

therefore
$$\mu = 2\cdot303 \times 10^5 \times \log\left(\frac{49\cdot45}{40\cdot84}\right)$$
$$= 19{,}120.$$

Growth increments for the females were 40·74 mm. in 1950 and 52·09 mm. in 1949 from which $\mu$ is found to be 24,580. The data for the females is less reliable, however, since it is based on smaller numbers.

From the data shown by Needham (1931, fig. 84), it may be seen that for growth processes a large proportion of the known values of $\mu$ lie between 17 and 21,000 with a smaller mode of 27,000, so that the calculated value appears quite reasonable, bearing in mind the scanty nature of the information. Therefore it may be concluded that the difference in mean size between the two year groups was most probably a temperature effect, though it is impossible to tell whether this might be direct or indirect.

### *Later Growth of the Males*

*The* 1949 *year group.* The form of the 1949 male population remained fairly constant throughout the winter with a clear peak at 6·25 cm. In March and April 1950 there was an increase in the 5·25 cm. group to form a shoulder on the main peak which probably represented the secondary peak at 4·75 cm. shown in the previous December catches (Fig. 5). By June these had grown a little and merged into the main peak. From July to October the graphs show steady growth until the now one-year-old group reached 7·75 cm. This corresponds to the peak at 8·25 cm. found in the trawl catches during October 1949. Again the discrepancy may be explained as a temperature effect, since it would be expected that with larger slower-growing prawns the difference would be less than with the O-group.

*The* 1948 *year group.* After October 1949 there was no further indication of more than occasional 1-year-olds in the catches, until the hoop-net catch from Paignton in February which shows (Fig. 7) a clear peak with the same mean length of approximately 8·25 cm. Again, in the spring this group was not taken by the trawls but it reappeared in the trap catches during May. In June the mean had risen slightly to about 8·75 cm. Subsequently, during July and August, trap catches were poor and there was no further sign of these prawns continuing their third year of existence.

### *Later Growth of the Females*

*The* 1949 *year group.* In separating the 1949 O-group from the autumn and winter trawl catches the complexity of the length distributions has already been noted. If we compare the 1949 October catches with those of January 1950 (Fig. 4), we see that a peak at 8·25 cm. has appeared in January, which at first sight might be attributed to growth of the 6·75 and 7·25 cm. groups. Although it showed up in three different catches from the Sound, this peak disappeared from the catches after January, and its origin must therefore remain obscure. By February the trawl catches having lost the 8·25 cm. peak show a pattern which would be expected if there had been little growth since October (Fig. 8). The hoop-net catch from Paignton gave a similar peak though with a slightly higher mean length. This was probably due to the smaller size groups tending to be restricted to the shallowest water, whereas the hoop-nets were shot chiefly around the 5-fathom line. In March and April only the smaller size groups are well represented in the trawl catches, presumably owing to the larger prawns migrating inshore first. It was not until May, when catches were made with baited traps as well as by hand-net, that a clear picture could be obtained. The population now becomes sharply divided, with the hand-net taking nearly all those below 6·5 cm. and the traps most of those above 6·5 cm., as shown in Fig. 4. Fig. 8B represents the mean of these two catches, giving a widely spread peak at 6·75 cm. The length frequencies of the 1949 year group in the trap catches were scaled up to percentages, and these were averaged with percentages in the hand-net catch, so as to eliminate the effect of this second peak in the trap catch. It was not possible to estimate the relative abundance of these two populations, and therefore this curve is by no

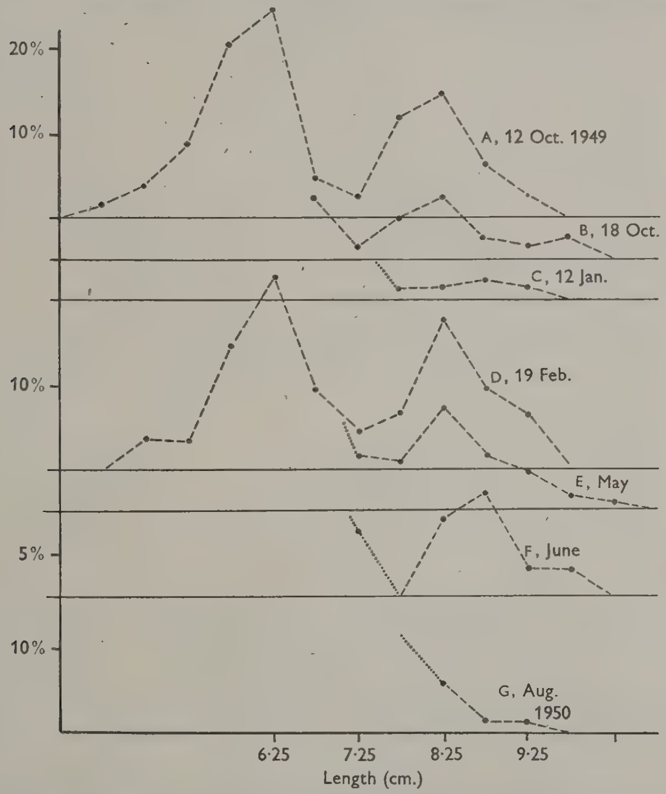

Fig. 7. *Leander serratus.* Length frequencies of 1948-year-group males (except in October and February the 1949 year group has been omitted). Samples taken by: A, trawl (67); B, trawl (16); C, trawl (18); D, hoop-nets (27), Paignton; E, traps (61); F, traps (18); F, hand-net (7).

means an accurate representation of the whole one-year-old group. It does, however, show the wide spread caused by the long breeding season and serves as a basis for comparison with later catches. A similar combined catch taken 3 weeks later (Fig. 8B) shows a peak at 7·25 cm. implying an average growth of half a centimetre. The difference between the means is actually 0·41 cm. After July the trap catches were poor, possibly due to the population moving closer inshore, so that growth can only be estimated from the hand-net catches (Fig. 10). These may at first be affected by an intermingling of the outer population, but the combined trap and hand-net catch (ratio 43–47) on 28 July (Fig. 9) is almost identical with the previous day's hand-net catch, the means being 7·44 and 7·35 cm. respectively. The hand-net catches may therefore be considered representative of the whole population, for by this time the places where the larger prawns tended to congregate had been discovered. Fig. 10 shows hand-net catches at approximately monthly intervals, chiefly from Rum Bay. By October there appears to have been fairly rapid growth so that the peak has moved up to 9·25 cm., slightly below that of the 1948 year group in October 1949 (Fig. 11), as would be expected.

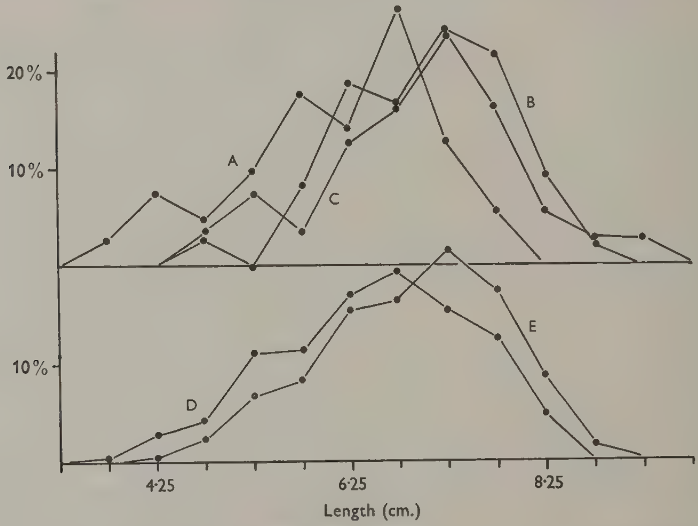

Fig. 8. *Leander serratus*. Above, comparison of catches of 1949 year group in October and February: A, October, trawl (123); B, February, trawl (37); C, February, hoop-nets. Below, two combined trap and hand-net catches. D, May 31; E, 24 and 27 June.

*The* 1948 *year group*. After October 1949 the largest size groups (8·75–10·75 cm.) which can now be ascribed to the 1948 year group, disappeared from the trawl catches. During February 1950, however, occasional catches of prawns were made by the research ships *Sula* and *Sabella*, chiefly after gales. These were composed of very large prawns, whose distribution curves showed peaks in the region of 10·25 cm.

A similar-sized catch was taken with lobster pots from an offshore ground near Dartmouth (see p. 354) and appeared to be representative of a fairly large population. The distribution curve presents a clear 'skew' pattern (Fig. 11, February), implying a selection against the smaller size groups. It is therefore likely that there is no significant difference between this group and that caught in October (Fig. 11), so that the bulk of these winter catches were probably composed of the 1948 year group. However, prawns above 11 cm. in length

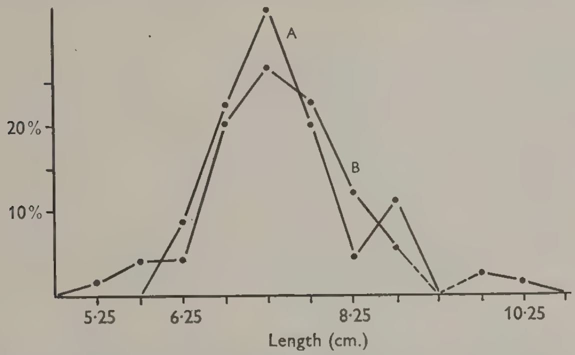

Fig. 9. *Leander serratus*. One-year-old females in July 1950 (see p. 344). A, hand net, 27 July. B, combined trap and hand-net catches, 28 July.

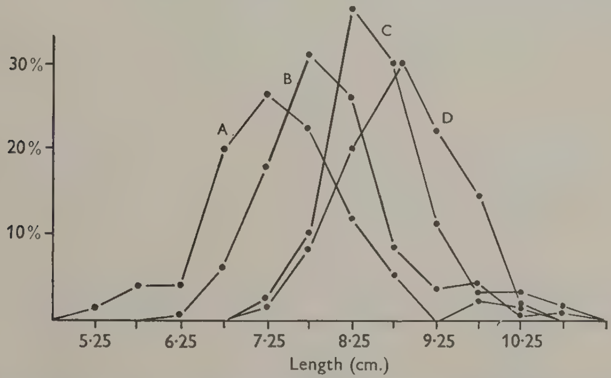

Fig. 10. *Leander serratus*. Length frequencies of the 1949 year group, July to October 1950. A, Rum Bay, July (75); B, Rum Bay, August (161); C, Rum Bay, September (59); D, average of catches from Drake's Island and River Yealm mouth, October (168).

were almost totally absent from Sound catches and may therefore have been older or have grown more rapidly than the inshore population.

This group also appeared during February in the hoop-net catch from Paignton, but in a rather smaller proportion, not forming a clearly defined peak.

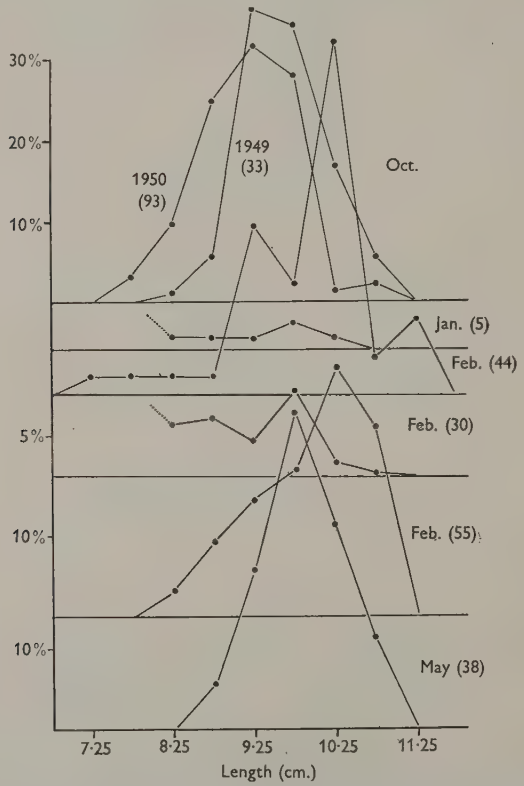

Fig. 11. *Leander serratus.* Length frequencies of 1-year-old females (see p. 345). The October and May figures are from fractions of catches scaled up to 100. October and January catches trawled in the Sound. February catches trawled in 20 fathoms (above), hoop-nets in 4 fathoms (centre) and lobster pots in 11 fathoms (below). May catch from traps inside Sound.

During spring and early summer the group shows up clearly in the trap catches (Fig. 11). There is no sign of any growth during the winter, the peak remaining at 9·75 cm. as in October. After July the trap catches declined and only occasional specimens were taken on the shore, therefore there was probably

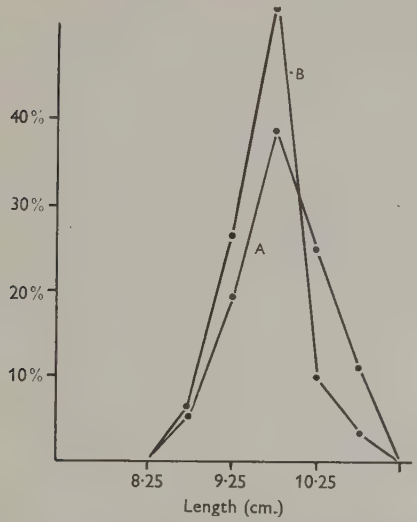

Fig. 12. *Leander serratus*. Comparison of trap catches of 1948 year group on (A) 19 and 31 May 1950 (36) and (B) 23 and 24 June 1950 (60), showing decline from 37% over 10 cm. length in May to only 10% in June.

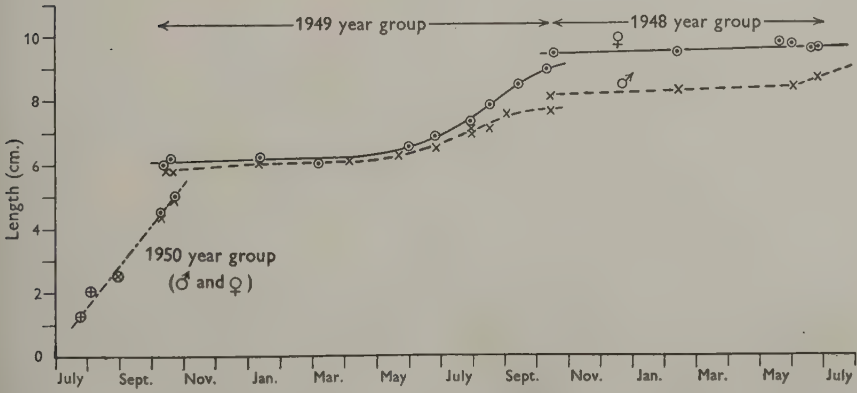

Fig. 13. Mean lengths of the various samples of three year groups, forming an approximate growth curve.

a considerable natural mortality at this time which may be related to the hatching of the last brood. Comparison of trap catches in May with those of June (Fig. 12), reveals a decline in the percentages of the two largest size groups from 37% over 10 cm. in length in May to only 10% a month later. This also appears to show a natural mortality, since there is no reason to presuppose any migration during this period.

The growth data have been summarized in Fig. 13 by plotting the mean lengths of the different year groups from October 1949 to October 1950. These results differ considerably from the conclusions on age and growth of this species reached by Nouvel and Van Rysselberge (1937), based on measurements of growth increments after moulting. At Plymouth there was little growth during the winter, though moulting continued. This may well be the case at Roscoff, since the sea-surface temperatures do not appear to differ by more than 1° C. (Lumby, 1935). Nouvel and van Rysselberge attributed the greater size attained by the females to an extra year's growth, but at least at Plymouth this is incorrect since the males' growth rate is less.

Sollaud (1916) had previously noted both the suppression of growth in the winter and the slower growth rate of the males, so that it is difficult to understand why Nouvel and van Rysselberge apparently took no account of his work. Sollaud, himself, gives a few figures for the growth of female *L. serratus* which he states live for 5 or 6 years. But unfortunately he gives no details of the data on which his conclusions were based.

Owing to variations in the distribution of the size groups no reliable estimates of mortality can be made.

## BREEDING

### *Males*

Little attention was paid to breeding biology of the male prawns owing to its relative uniformity among the Natantia. Maturity is reached at an early stage, since during December a ripe female prawn in a tank with several small males in the 40–44 mm. group (i.e. 6–7 months old) became berried, showing that one of these had become capable of successful fertilization.

### *Females*

Data on the breeding of female prawns is summarized in Fig. 14; grouping by length is justified since it has been shown that there was little growth during the winter, while towards the end of the breeding season growth shown in the graphs can only be due to those females which have hatched their eggs. In Fig. 14 the 1949 year group is divided into four 1 cm. groups up to 8·4 cm., the 1948 year group being represented by the 8·5–9·4 and 9·5–10·4 cm. groups. Only the two smallest groups show non-breeding or neuter individuals throughout the whole period. In the 4·5–5·4 cm. group only one berried female was taken: therefore those which possessed a maturing ovary probably

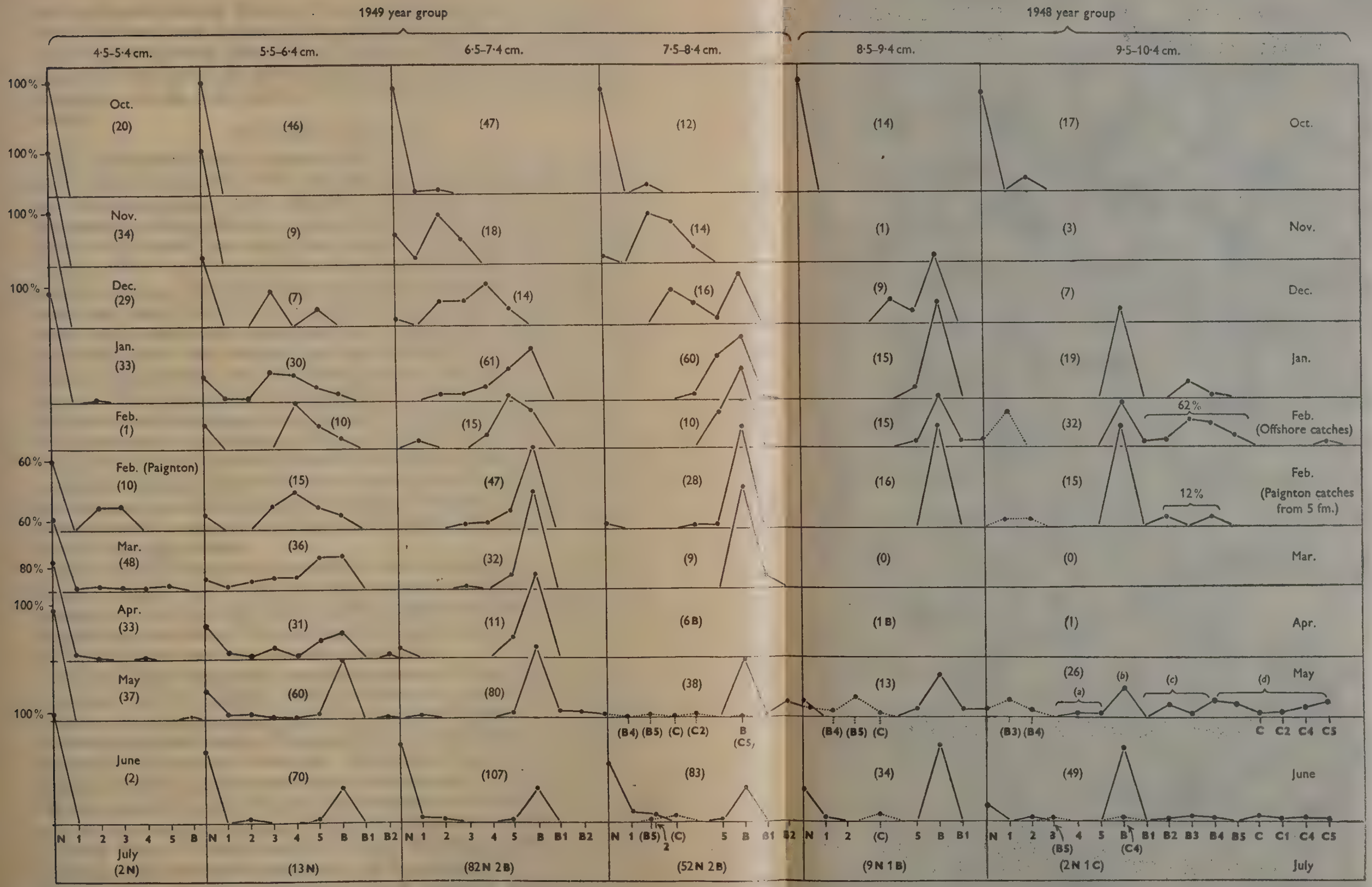

Fig. 14. *Leander serratus.* Seasonal abundance of various breeding stages through the year. **N**, neuter (i.e. ovary not externally visible); **B**, berried (egg-bearing); **C**, cemented (egg membranes attached to pleopods), this stage lasts only about 3 days after the eggs have hatched. 1–5, arbitrary stages in maturation of the ovary: 1, ovary small, white and translucent; 2, ovary green, area about one-eighth of carapace; 3, ovary green, area about one-third of carapace; 4, ovary green, area about two-thirds of carapace; 5, ovary ripe, filling carapace and extending into first abdominal segment. (*a*) neuter intermoult after hatching first brood; (*b*) 2nd brood; (*c*) ovary ripening for third time; (*d*) possibly very late first spawners or advanced second spawners.

grew sufficiently during March and April to be included in the next larger group. The next three sections (5·5–8·4 cm. inclusive) show that with increase in size spawning takes place earlier: February for the 5·5–6·4 cm. group; January for the 6·5–7·4 cm. group; and December for the 7·7–8·4 cm. group. Correlated with this is the increase in the proportion which produce a second brood.

### *The Period of Egg-Carriage*

The approximate time of spawning may be deduced from Fig. 14 as the point where the majority of any one particular group change from showing ripe or ripening ovaries to the 'berried' condition. The end of the period of egg-carriage is more difficult to ascertain since, unless the ovary ripens again for a second brood, the animal may hatch its eggs and moult, remaining 'cemented' for only 2–4 days. Thus only small numbers of cemented females may be expected. Notes were kept of the number of females whose eggs were nearly hatching as shown by the transparency of the eggs, all the yolk having been used up, and by the conspicuous eyes of the embryos. During the first intermoult period after hatching the eggs, the length of the epimera or side plates of the abdomen was considerably greater than that of non-breeding females. This gave a method of separating those of the 5·5–6·4 cm. group which had just finished breeding in June, from non-breeding individuals. The period of egg-carriage for the majority of the 5·5–6·4 cm. group is thus considered to have lasted from the beginning of March till the end of June, or approximately 4 months; bearing in mind that in the spring the smaller prawns were growing and some may have been included in this group. Similarly, for the 6·5–7·4 cm. group about 85% spawned in January and February, whilst the most advanced hatched their eggs in May.

Thus for both these groups the period of egg-carriage appears to have been about 4 months. The 7·5–8·4 cm. group spawned chiefly in December and January, but in April, when some hatching might have been expected, only six specimens were taken. Thus the length of egg-carriage cannot be estimated, for by May some may have spawned a second time.

The two largest size groups comprising prawns of 8·5–9·4 and 9·5–10·4 cm. (including the few specimens which exceeded 10·4 cm.) could not, unfortunately, be caught throughout the whole season, so that results are incomplete. Spawning probably began in November, since the few specimens obtained in December were almost all berried. Information also came from lobster fishermen that they had first taken berried prawns about 7 November. Another lobster pot catch from the same area was examined on 18 February when about 3% had eggs ready to hatch, and altogether 90% showed ovaries ripening for a second brood. From the state of the eggs it seemed unlikely that much hatching would have taken place before the beginning of March. Here again the period of egg-carriage appeared to be about 4 months. Another February sample of these two size groups was obtained with hoop-nets at Paignton in shallow water (less than 5 fathoms), only 12·1% of which contained ripening ovaries. Development appears therefore to be retarded under inshore conditions, possibly associated with slightly lower temperatures. In March and April no catches were obtained, and it was not until May that the traps supplied reasonable samples. Referring to Fig. 14, the patterns shown in May and June are rather complex, which in part may be due to a mixture of the stock after those from the deeper water had migrated inshore. The non-berried females with a ripening ovary are clearly passing through a neuter intermoult period after hatching their first brood; however, berried females up to stage 3 would be expected to be carrying their second brood of eggs, with the most advanced showing signs of a forthcoming third spawning. Since it has been shown that there was little hatching in February, the berried females in stage 5 in May and the cemented females could not be hatching their second brood and may possibly represent that part of the population which overwintered inshore lagging behind the offshore population by more than a month. It is unlikely that the difference in temperature between 5 and 15 fathoms is more than 1° C. (Dr H. W. Harvey, personal communication) which would account for a lag of only 2½ weeks, taking $\mu$ for development as 20,000 (Needham, 1931, p. 521). Therefore other factors are probably involved. One possibility is that the maturation of the ovary is connected with the offshore movement, so that those whose ovaries are slower in development have in some way less tendency to move offshore.

During June the appearance of neuter females marked the end of spawning for 28 and 14% in the 8·5–9·4 and 9·5–10·4 cm. groups respectively. In July the trap catches declined and contained only occasional non-breeding members of these two largest groups. Possibly many died after hatching their eggs, but since Lebour (1947) found larvae in September and October in 1944, a few of these may survive, perhaps hidden away in slightly deeper water.

Sollaud (1916) stated that the females of *L. serratus* did not mature until the end of their second summer, and some not until the spring of their third year. This would imply that on the French coast this species takes very much longer to mature. But, as with his statements on the age and growth, no hint is given of the data on which he based them.

*The production of eggs.* Only a few egg counts were undertaken to estimate numbers of eggs produced by the largest and smallest females, since Höglund's

TABLE I. NUMBER OF EGGS PRODUCED BY SMALL AND LARGE PRAWNS

| Length (cm.) | No. eggs | Length (cm.) | No. eggs |
|---|---|---|---|
| 6·2 | 1523 | 9·3 | 3887 |
| 6·8 | 2106 | 9·6 | 3150 |
| 7·0 | 1628 | 10·4 | 3859 |
| 7·1 | 1989 | 10·5 | 4282 |

extensive egg counts on *L. squilla* have shown a logarithmic relationship between body size and number of eggs, dependent presumably on the increase in volume of the carapace.

## Distribution and Migrations

The geographical range of *L. serratus* extends from Britain to the Mediterranean (Kemp, 1910), with the region of the Wash marking its northern limit.

### *Metamorphosis of the Larvae*

No systematic collection of larvae from the plankton was attempted. Instead, watch was kept for the post-larval and young stages. Trawling with a stramin net lashed to the cod-end of a 6 ft. beam trawl worked from the *Gammarus* was carried out in the Sound at the end of May in depths of 4–5 fathoms, fairly close to the rocks. No young prawns were taken. Agassiz trawl catches during June from depths of 10–20 fathoms were also examined without success. Post-larval stages, together with late-stage larvae, were first obtained from pools at or above mid-tide level in July. Sollaud (1916) had previously noted this on the French coast. It was shown while analysing these catches (Fig. 1, C, D) that the smallest stages were virtually absent lower down on the shore at about low-water springs. Since settlement was almost certainly still going on at that time (3 August) it seemed that metamorphosis usually occurred high up in the littoral zone. At first sight it might appear that the larvae, which are fairly widely distributed throughout coastal water, since they have been recorded from near the Eddystone (Russell, 1927) where no prawns are taken by the lobster fishermen, would have to perform a definite migration to reach the shore. But the tidal streams running to and fro along the coast probably set up eddies around headlands and other obstacles sufficient to sweep many larvae inshore at one time or another. It might be possible for the larvae once in the right zone to maintain their position and so avoid being swept away before metamorphosis.

In this respect the work of Sollaud (1923) is of interest. He found, at Roscoff, that laboratory-reared larvae usually had eight stages or moults, but that larvae from townettings almost always metamorphosed at a size similar to his fifth stage. Gurney (1924) drew attention to these facts, but considered the extra stages anomalies associated with the artificial conditions. It seems, however, more reasonable to assume that this is another instance of the capacity of many larvae to postpone metamorphosis until they find suitable conditions.

### *Distribution of the O-Group*

*Autumn and winter.* From July until the end of October the young O-group prawns remained abundant on the shore. Towards the end of October they became less numerous and after the beginning of November very few could be taken in either 1949 or 1950. At Trevol pier where conditions, though estuarine, were very sheltered, the larger prawns disappeared in October, but some of those in the smallest size groups remained till the end of November.

Throughout the winter (1949–50) the males of the 1949 year group, 5–7 cm. long, formed the bulk of the trawl catches in the Sound. The best catches were obtained from 'White Patch' area, and from inside the Breakwater, in depths of 4–5 fathoms. The smaller members of this group showed up in the trawls from Mount Batten (shallow water 1–2 fathoms and rocky bottom) as a separate peak, which did not appear with the rest of the trawl catches in slightly deeper water and on softer bottoms.

Perhaps the most notable feature of the winter catches was the relative scarcity of the females. In catches from 'White Patch' and the Breakwater the sex ratio was between three and four males to one female; whereas it will be shown that during the summer when the whole population was close inshore there was a slight majority of females. Therefore it seems probable that during the winter the females, many of which were berried, tended to remain in the greater seclusion of the rocks. This view was supported by the result of the hoop-net catch at Paignton (on rocky bottom) during February when the sex ratio was approximately one male to two females. Poulsen (1946) gave a similar interpretation to the sex ratios obtained with *Nephrops norvegicus*. Conditions at Paignton differed from Plymouth in that the rocks were fringed by fairly clean sand, and sheltered from the south-west. Trawls were made close to the rocks but without taking any prawns. There was thus very little offshore migration at Paignton; the only difference between summer and winter distribution being that part of the population spread into the littoral zone in summer, but not in winter or spring.

On more exposed coasts where the rocks extend into deep water the prawns would doubtless move farther offshore; evidence for this was found only in the older year groups.

The only 1949 autumn catches where the females outnumbered the males were from the Tamar estuary, the results total 36 ♂♂ against 77 ♀♀, which, on the expectation of even numbers, would occur by chance less than one in a hundred times. However, since the males were found to penetrate well into the estuaries during the summer (1950), it appears that they tended to leave them in the autumn before the females. Lloyd & Yonge (1947) found that *Crangon vulgaris* behaved in much the same way, and showed that the males were more susceptible to combined low temperature and salinity (i.e. winter conditions) than the females. Pannikar (1941) found that in *Leander serratus* the osmotic pressure of the blood scarcely differed between males and neuter females, but did not apparently differentiate the sexes in studying the capacity for osmoregulation.

*Spring and summer.* During March and April the majority of the females from 6·25 to 8·25 cm. gradually disappeared from the trawl catches. Presumably they were the first to migrate inshore. Prawns were first caught with a hand-net from the shore on 3 May, and thereafter in fair quantities. Unfortunately it was not possible to correlate this with a simultaneous disappearance from the trawling grounds, but only occasional prawns were taken during several trawls in June.

In 1949 the inshore migration must have occurred much earlier, since numerous prawns were found in shore pools at Wembury at the end of March. *Aplysia punctata* was also abundant at this time, but only a very few appeared inshore during the spring of 1950. Sea-surface temperatures in the Sound were almost exactly similar for the two years, as were the air temperatures. Temperature therefore cannot have been the decisive factor in the cause of these migrations.

During early summer prawns also moved up the estuaries and by July they were being fished commercially off Saltash. Percival (1929) studied the estuarine distribution of three species of *Leander* including *L. serratus*.

At Rum Bay where most of the trap catches were made, the separation of the females into two apparently distinct populations has been noted (p. 343). For instance, of the females caught on 31 May, the hand-net took specimens almost entirely less than 6·5 cm., while the traps scarcely took any below this length (Fig. 4, May.) This segregation was scarcely noticeable among males, however, except that the hand-net took a much larger proportion of the 5·75 cm. group than the traps.

### *Distribution of the* 1-*Year-Old Group*

After July the trap catches declined, suggesting that the whole population was close inshore, mostly within the 2-fathom line, and at Paignton within about 4 fathoms. No change in this distribution apparently occurs until October when, according to local tradition, trawling starts (information supplied by Mr W. Searle). However, in the Hamoaze, especially below Saltash, trawling is sometimes successful in late August. Prawn trawling usually started near Saltash and moved downstream to Torpoint, West Muds and Drake's Island, finishing in Jennycliff Bay and inside the Breakwater. Thus there would appear to be, as the fishermen believe, a migration of the prawns away from estuarine conditions; this would be expected from the well-established fact that tolerance of low salinity decreases markedly with temperature in most decapods (Lloyd & Yonge, 1947). Several trawls were made in the Hamoaze during winter with, as might be expected, negative results, but there was always the possibility that the prawns managed to hide away in places inaccessible to the trawl. Preliminary work on tagging was also undertaken to try to verify the migration, but although a method was worked out it proved impracticable to mark sufficient numbers for a reasonable chance of returns.

In the Sound, apart from the first successful trawl in October 1949 (Figs. 4 and 5, October), only very small numbers of the 1-year group (9–11 cm.) were taken throughout the winter. They reappeared, however, in the hoop-net catch from Paignton and the trap catches during the spring, when both sexes seemed to be restricted to a rocky bottom.

During the winter prawns were occasionally caught by *Sula* and *Sabella* on trawling grounds outside the Sound both with the otter trawl and the finer-meshed Agassiz trawl. During February, however, larger catches of up to fifty were made, chiefly after gales. These trawl catches from depths around 20 fathoms, which consisted almost entirely of large female prawns, have been discussed on p. 345. It is unlikely that they represented more than scattered offshoots from the main population. Quite large quantities of prawns were caught by lobster fishermen on various grounds between Berry Head and Start Point from November till the end of March, at a depth of about 10 fathoms. Since these grounds were fished almost all the year round and no prawns were caught during the summer, there must have been an offshore winter migration. The distance between the 5- and 10-fathom lines is about half a mile in this area. The population as sampled by the lobster pots appeared to be wholly female. Out of a catch of some 200 prawns observed during an expedition with the fishermen, all were females. Several pots were partially covered with prawn netting so that if only small males had been present, some at least would have been retained. The disappearance and presumed inshore migration towards the end of March may therefore be related to the hatching of the first brood of eggs, mating, and the second spawning. The basis of the orientation necessary for even a short migration remains inexplicable.

During their third summer this group was well represented in the trap catches in the Sound until July (Fig. 4). Afterwards the catches declined and there was probably a high mortality after the second brood had been hatched.

## FOOD

A note of the stomach contents of *Leander serratus* has been given by Hunt (1925). With further study it was hoped to ascertain how the food varies at different times and in different places. Also it was of interest to see whether the feeding habits differed from those of *L. squilla*, since these two species overlap in their distribution on the shore.

The stomachs were removed within a day or so of collection and preserved in formalin. Most of the contents were lost if the prawns were placed in formalin while still alive. It was usually found possible to distinguish the more freshly filled stomachs from those in which the food had been subjected to a period of grinding or churning, since the latter tended to appear, under a binocular microscope, as a homogeneous mass giving off clouds of minute particles. Any of this type were discarded. The contents were first examined with a low-power binocular and the larger fragments or animals noted, the remainder being usually subsampled by pipetting a drop of the material on to a slide and examining under higher magnification.

### *Notes on the Stomach Contents*

*Debris.* This category includes all unidentifiable finely divided material. The name is used in place of the more usual 'detritus', since it was not known whether most of the material was organic or inorganic. It was not always possible to decide whether the debris had been ingested as such or ground up in the stomach. Much churning and grinding does, in fact, take place and may be observed most readily in the smaller and more transparent prawns. Debris was more abundant in the stomach contents of trawl catches from the muddy grounds of the Sound than from elsewhere. Since it was found from aquarium observations that a muddy substratum was not ingested at random, some at least of the debris may well have been eaten accidentally with, say, algal fragments.

*Algae.* In all inshore catches algae usually formed a considerable part of the stomach contents. During autumn and winter the algal material found in the stomachs of trawl-caught prawns consisted chiefly of unpigmented fragments of thalloid algae which were probably derived from decaying *Laminaria* plants. In hand-net catches, green, thalloid and filamentous fragments were common, also occasionally brown filaments. Hoop-net and trap catches from slightly deeper water showed, as might be expected, more red forms, chiefly filamentous.

*Crustaceans.* Small crustaceans nearly always formed a significant proportion of the diet. Indeed the stomach contents of one off-shore trawl catch consisted almost wholly of small decapods, while the young O-group prawns very commonly fed on ostracods. Fragments of cuticle were very often found, and when ground up may have formed part of the 'debris'. It was often difficult to distinguish whether cuticle fragments of, say, a small amphipod represented parts of a 'moult' or the remains of a whole animal. When any trace of fleshy material was observed it was assumed that the whole animal had been consumed. Copepods proved particularly difficult in this respect, so that records of them may be unreliable.

*Molluscs.* Only one species of mollusc appeared in the stomach contents more than occasionally; this was *Odostomia plicata*, which Fretter & Graham (1949) have shown to be probably ectoparasitic on *Pomatoceros*. These tiny gastropods were found chiefly in prawns trawled from near the Hoe. It would seem that they must be fairly common judging from the fact that one large prawn had thirty-one in its stomach. There was a surprising absence of other small gastropods which are usually abundant on algae during the summer.

*Other groups.* Foraminifera occurred fairly often in the stomach contents but rarely in significant numbers. Small polychaetes were also found occasionally, rather less frequently than might be expected. Unidentified eggs and algal spores sometimes appeared, often in considerable numbers in just one stomach out of a sample. Doubtless almost any post-larval or young stages under 2 mm. would be taken when available.

TABLE II. THE STOMACH CONTENTS OF *LEANDER SQUILLA* AND O-GROUP *L. SERRATUS* TAKEN FROM THE SAME POOL

(+ + +, 75–100 %; + +, 40–75 %; +, 40 % (all very approximate); tr., very little.)

| No. | Debris | Filamentous algae | Thalloid algae | Grit | Cuticle fragments | Foraminifera | Copepods | Ostracods | Mites | Miscellaneous |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *L. squilla* | | | | |
| 1 | + | + + | .. | + + | .. | 13 | .. | .. | .. | .. |
| 2 | + | Brown and red | .. | .. | + | 2 | .. | .. | .. | .. |
| 3 | + + + | + | .. | .. | .. | 7 | | .. | .. | .. |
| 4 | + + + | + | .. | + | .. | 7 | .. | .. | .. | .. |
| 5 | 97 % | .. | .. | .. | .. | 1 | .. | .. | .. | 1 small gastropod |
| 6 | 85 % | + | .. | .. | + | 2 | .. | .. | .. | .. |
| 7 | 10 % | Few red fils | 90 % green | .. | .. | .. | .. | .. | .. | .. |
| 8 | + | + + | .. | tr. | .. | .. | .. | .. | .. | .. |
| 9 | 80 % | + | .. | .. | + | .. | .. | .. | .. | .. |
| 10 | 90 % | .. | Green | tr. | .. | .. | .. | .. | .. | .. |
| 11 | .. | .. | .. | .. | .. | .. | .. | .. | .. | Many? nematode cuticles |
| 12 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| 13 | tr. | tr. | 90 % green | .. | .. | .. | .. | .. | .. | .. |
| 14 | .. | + + | + + | + | .. | .. | .. | .. | .. | .. |
| 15 | .. | .. | .. | .. | .. | 1 | Several | .. | 1 | 1 chironomid cuticle<br>1 gastropod |
| 16 | + + | + | .. | .. | .. | .. | 1 moult | .. | .. | 1 amphipod moult |
| | | | | | | *L. serratus* | | | | |
| 1 | tr. | .. | .. | .. | .. | .. | 4 moults | 1 | 1 | 1 chironomid cuticle, 1 gastropod |
| 2 | 75 % | tr. | .. | .. | + | .. | .. | 1 | 1 | .. |
| 3 | 80 % | .. | .. | .. | + + | .. | .. | 1 | 1 | 1 chironomid cuticle, 1 amphipod head |
| 4 | 50 % | .. | .. | + | 30 % | .. | 2 moults | .. | 1 | .. |
| 5 | .. | .. | .. | .. | + | .. | 2 | 1 | .. | 1 amphipod moult |
| 6 | tr. | .. | .. | .. | .. | .. | 1 moult | 3 | .. | .. |
| 7 | + | .. | .. | .. | + | .. | 12 copepodites | .. | .. | .. |
| 8 | tr. | .. | .. | .. | + + | .. | .. | 4 | .. | .. |
| 9 | 75 % | .. | .. | tr. | .. | .. | .. | 4 | .. | .. |
| 10 | 85 % | .. | .. | .. | .. | .. | 3 moults | 1 | .. | .. |
| 11 | tr. | .. | .. | .. | + + | .. | .. | 2 | 1<br>2 moults | .. |
| 12 | + | .. | .. | .. | .. | .. | .. | 2 | 1 | 1 chironomid cuticle |
| 13 | + | .. | .. | .. | .. | .. | 3 moults<br>1 copepodite | ..<br>1 | .. | .. |
| 14 | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. |
| 15 | 85 % | tr. | .. | + | .. | .. | .. | 4 | .. | .. |
| 16 | + | + | .. | .. | + | .. | 4 moults | 9 | .. | Pt. of 1 isopod, 1 gastropod, 1 chironomid cuticle |
| 17 | 70 % | .. | .. | .. | + | .. | .. | 2 | .. | .. |

*The food of the O-group.* The food of young prawns less than 30 mm. in length differed rather strikingly from that of larger specimens, notably in the absence of algae and presence of large numbers of ostracods. The exact reverse was found with a sample of *Leander squilla* taken from the same pool (Table II) which fed chiefly on algae, with some foraminifera but no crustaceans. Both species took a fair amount of debris, of which there was ample.

Otherwise there was a clear divergence of feeding habits as would be expected from the theory of closely related species occupying the same habitat.

The stomach contents of about 140 *L. serratus* have been analysed, and show that the food varies from place to place and throughout the year. In general, the species is omnivorous. Algae and small crustaceans appear to form a large proportion of the diet. Much debris was also found in the stomach contents, but there is no reason to consider it of more than slight food value. A great deal more must be known of the digestive powers of prawns and of the composition of the food organisms before definite conclusions can be drawn. It is also impossible to ascertain whether the animals found in the stomach have been captured dead or alive, but since observations have shown that prawns can catch small amphipods and other crustaceans, it may be that their habits are not so much scavenging as is commonly supposed.

## NOTES ON BEHAVIOUR

Tidal and diurnal migrations at Rum Bay have been observed. On this shore, which may be taken to represent any fairly sheltered rocky coast, prawns are first seen 2 or 3 hr. before low water walking or swimming over the algae moving out with the tide. Where the shore has been eroded into tiny bays and gulleys they often form a steady procession. The larger prawns usually leave first, keeping in 3 or 4 ft. of water, and creeping under weed or rocky ledges where possible and thus are less easily observed. Last to leave are the baby O-group prawns usually so numerous as to form a steady stream swimming vigorously only a foot or so below the surface. Three-quarters or half an hour before low tide the migration has ceased and most of the prawns are hidden under *Laminaria* fronds or congregated under ledges or in tunnels, anywhere sheltered from light. Very soon after the tide turns the O-group begin to move in with it, but the larger prawns do not usually return until the water is 4 or 6 ft. deep.

During the night there is a migration up the shore, since prawns may be observed with a torch right up in the barnacle zone where they normally never appear by day. The eyes show up very brightly by torchlight, glowing with a fascinating golden iridescence, as was noted almost 100 years ago by Warrington (1855). This is well known to many fishermen since they may be caught readily at neap tides in this way.

Prawns in the deeper part of the *Laminaria* zone can be caught only in hoop-nets or traps after dark, the first being taken usually just after dark. This is a marked difference in behaviour from those on the shore which are definitely attracted to a piece of fish bait in the daytime. It is probable that those in the deeper water remain hidden away during the hours of daylight, which may be related to the presence of predators such as bass, pollack and cuttlefish in this zone.

In spite of their prominent eyes repeated observations show that prawns appear to make little use of them. The antennal signal reaction to a moving object is occasionally shown, but normally there is only a slight twitch or wave of the antennae without relation to the direction of the object. A sudden movement or change in light intensity will often cause the escape reaction, i.e. a series of vigorous backward flaps of the abdomen.

Food seems to be located first by scent and then by the antennae, since a prawn may even walk right over a piece of food if the antennae have failed to touch it.

Mating also appears to be a response to chemical stimuli, associated with the soft cuticle of a recently moulted female with a ripe ovary, since the males are only attracted to females in this state (Höglund, 1943; Burkenroad, 1947). If an 'attractive' female is placed in a tank with males nothing happens until the antenna of a male touches some part of the female. At once the male's behaviour alters, he swims very rapidly in no particular direction, often making small circles, until he again makes contact even though the female had been only a few centimetres away. As this was frequently observed, it seems that the male can have no visual perception of the female.

## SUMMARY

An attempt has been made to follow the post-larval life history of *Leander serratus* through 1 year.

Growth has been followed from length measurements of numerous samples of populations obtained by several different methods. Owing to the length of the breeding season and especially to the differing habitat preferences of the various size groups in the littoral and sublittoral zones, estimates of their rate of growth are necessarily approximate.

After metamorphosing, apparently in very shallow water, during July the O-group grew rapidly, their average length by October being in the region of 5 cm. There was a marked difference in length between the October catches of 1949 and 1950, and reasons have been given for correlating this with the differing temperatures of these 2 years. Growth almost ceased during the winter, and not until June was there a marked change in the size frequencies. In their second summer's growth females outstripped the males, the mean lengths in October being approximately 9 and 7·5 cm. respectively. There appeared to be a very high mortality in the third summer, with scarcely any surviving to the autumn. However, occasional extra large prawns were trawled during the winter so that a definite conclusion on the limit of age is impossible.

The breeding season, judged by the presence of berried females, lasted from November until June (1949–50). Maturity in the smallest males of the O-group was reached at least in December and with the smallest females in March.

With increase in size spawning took place earlier and the numbers which spawned twice increased. Some of the largest prawns may have produced a third brood. The period of egg-carriage was about 4 months at roughly 9–11° C.

The distribution in winter varied according to the habitat. There was a tendency to leave the estuaries. In the Sound the male prawns were widely distributed in depths of 4-5 fathoms on a muddy bottom, while the females, judging from their scarcity in the trawl catches, were more restricted to the rocky parts. The spring inshore movement took place during April and May, with some variation between different years, apparently unrelated to temperature. During early summer, trap catches showed a marked discontinuity in the distribution of the size groups, the larger prawns being taken only in the sublittoral zone. On exposed rocky coasts prawns overwintering the second time moved into deeper water, from 10 to 15 fathoms, and have sometimes been of value to lobster fishermen.

Examination of the stomach contents, though often difficult, showed that the species was in general omnivorous. Algae and small Crustacea appeared to be the chief sources of food. Much debris was also taken; this is tentatively considered of lesser importance.

Small-scale tidal and nocturnal migrations have been observed. The results of catches with baited traps show that prawns in the sublittoral zone tend to be markedly nocturnal in their habits, compared to those observed on the shore.

From laboratory and field observations the eyes are thought to be of much less use than their size would suggest. Prawns may perceive sudden movements visually, but they cannot apparently avoid obstacles, locate pieces of food, or in case of the males find a mate, without the use of their antennae.

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# NOTES ON *LEANDER SQUILLA* L.

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From the Plymouth Laboratory

(Text-figs. 1–5)

After the monograph on *Leander squilla* by Höglund (1943) in Sweden, any further work might seem repetitive; however, at Plymouth some differences in the biology of this species have been noticed, as might be expected from the different climates. It has been thought worth while to record these additional notes on the age and growth, together with records of the food.

De Man (1915) has separated the Scandinavian population as the forma *typica* from those of Holland, France and Britain, which he grouped into the variety *intermedia*, the only distinctive character being the length of the carpus of the second leg relative (either longer or shorter) to that of the chela. It is not known whether the two forms intergrade.

## HABITAT

*L. squilla* is widely distributed in Plymouth Sound and in the river estuaries, being most abundant in the upper shore pools. Around harbour walls and pier piles where it occurs with *L. serratus* there is usually a segregation, *L. squilla* keeping in the shallower water. This was noted many years ago by Sinel (1906) at Jersey. It also appears to be less tolerant of wave action than *L. serratus*, being rare in more exposed localities. During the winter *L. squilla* tends to be scarce in the estuaries but remains in the shore pools and is scarcely ever taken with the prawn trawl. This contrasts with its behaviour in the Clyde (Elmhirst, 1921) and in Sweden (Höglund, 1943) where there is an offshore winter migration; and is presumably related to the warmer temperatures prevailing at Plymouth. (Mean sea surface temperatures in February: Plymouth 7 to 8° C., Millport 6° C., Kristineberg −1 to +1° C.)

## AGE AND GROWTH

Spawning took place towards the end of April in 1950, and continued well into August, for of the females caught on 16 August 57% were berried. Since the period of egg-carriage would not be more than 6 weeks (data from Höglund, 1943), it is possible that a third brood may be produced. The post-larval stages first appeared on the shore during the second week of August, a month later than those of *L. serratus*. By October the mean lengths for the O-group were: 1949, males 2·54 cm., females 2·95 cm.; and in 1950, males 1·85 cm., females 2·12 cm. Thus there is a clear divergence between the 1949 and 1950 year groups which, as with *L. serratus* (see Forster, 1951), may be ascribed to the difference in temperature conditions between the two years. As a check, from these figures the temperature characteristic $\mu$ can be calculated as shown by Needham (1931). Using the average sea temperatures 17·27° C. in 1949 and 15·57° C. in 1950, values of 34,140 (females) and 31,320 (males) for $\mu$ were obtained, instead of 17,000–21,000 as would be expected from the large numbers of already known values of $\mu$ for growth processes. However, it must be remembered that these young *L. squilla* are found in upper shore pools, and at high tide may move into shallow water so that they are affected to a considerable extent by air temperatures. On Plymouth Hoe (height 108 ft.), average air temperature from August to October (inclusive) was found to be 16·50° C. in 1949 and 13·76° C. in 1950. Using these figures $\mu$ comes to 20,020 for females and 19,160 for the males. It seems therefore that in the shallow-water conditions under which this species lives the effective temperatures are those of the air rather than of the sea surface.

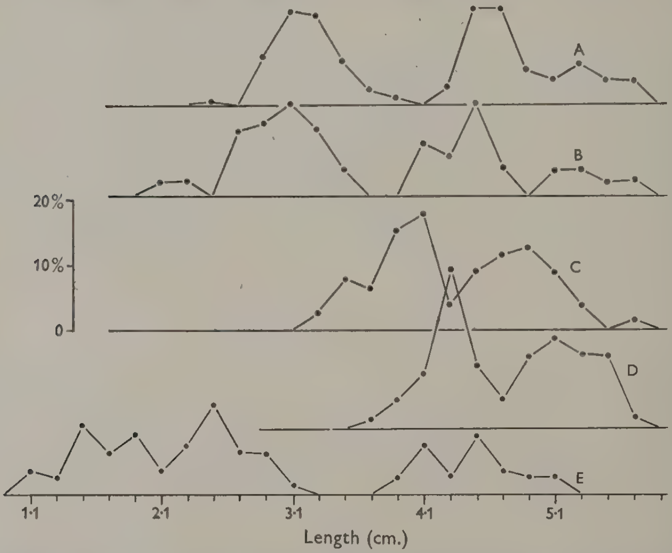

Fig. 1. Length frequencies of female *L. squilla*. A, Trevol, October 1949 (178); B, Rum Bay, October 1949 (50); C, Trevol, April 1950 (79); D, Trevol, August 1950 (73); E, Rum Bay, October 1950 (81).

Figs. 1 and 2 show the percentage size frequencies of various samples of

*L. squilla.* The samples from Trevol Pier, situated in a creek off the Tamar estuary, differ considerably from those from Rum Bay, in the Sound (Table 1).

In 1949 the O-group males, unlike the females, did not penetrate the estuary, being virtually absent from the Trevol catches. This compares with the observations of Lloyd & Yonge (1945) on *Crangon vulgaris*, who found that the males tended to inhabit more saline conditions than the females. In an estuary, where the surface water may at times be of low salinity, the males might well keep in slightly deeper water and so affect the sex ratios of samples taken with a hand-net. The sex ratios found in the Gullmar Fjord by Höglund have been

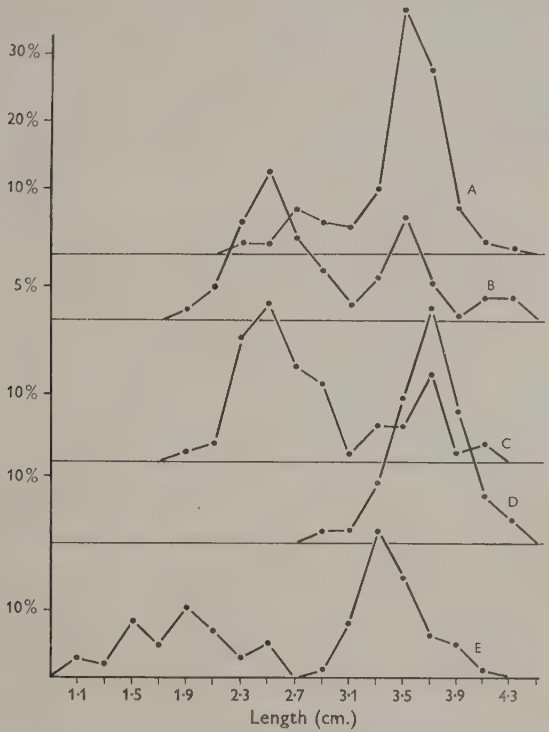

Fig. 2. Length frequencies of male *L. squilla*. A, Trevol, October 1949 (133); B, Rum Bay, October 1949 (123); C, Rum Bay, November 1949 (77); D, Trevol, April 1950 (56); E, Rum Bay, October 1950 (102).

TABLE I. SEX RATIO: PERCENTAGE OF MALES

| | | | | | |
|---|---|---|---|---|---|
| Trevol Pier | 41 | 13 | 43 | 48 | — |
| Rum Bay | 63 | 64 | 58 | 73 | 51 |

plotted in Fig. 3 as the percentage of males. Although he has attributed the fluctuations solely to chance, it may be seen that this is very unlikely owing to the extent of the fluctuations and the manner in which the points reinforce each other. The two years differ considerably; in 1940 there appears to be a steady decline in the percentage of males, whereas in 1941 there was a more rapid decline partly due to the 1939-year-group males disappearing, followed by further large fluctuations. In both years the females of the O-group appeared at first in much greater numbers than the males. It would have been interesting to compare the rainfall of the two years to see whether any correlation with the sex ratio could be traced, but no data are available.

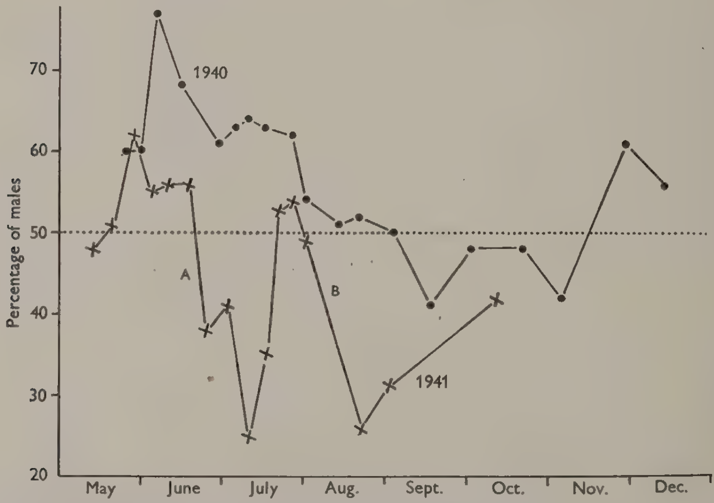

Fig. 3. Percentage of males in catches from Sweden (data from Höglund, 1943). A, 1-year-old males disappearing; B, 'O-group' females arriving.

Variation in the stock from place to place was apparent from a sample from Paignton harbour taken on 21 November which in both males and females showed one very dominant group, presumably the O-group, but with a mean length approximately 4 mm. greater than that of a comparable catch from Trevol Pier (Fig. 5). Whether this represented a difference in growth rate or in the method of sampling is unknown.

The growth of females is shown in Fig. 4, together with Höglund's data on age and growth. Growth is seen to continue throughout the year at Plymouth in contrast with the complete cessation found by Höglund. This appears to be correlated with the temperature of the sea which is much lower in winter and higher in the summer in Sweden. Also the 2-year-olds appear to have grown

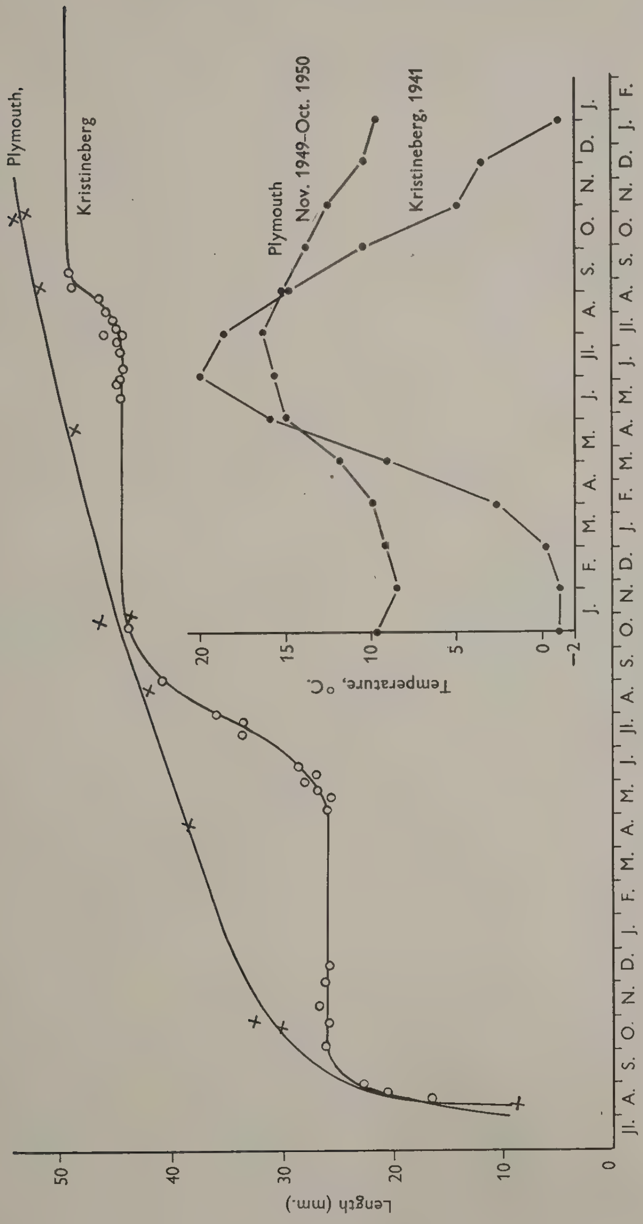

Fig. 4. Age and growth curves of *L. squilla* at Plymouth and in Sweden, together with sea-surface temperatures. Swedish data from Höglund (1943).

somewhat larger at Plymouth. As with *Leander serratus*, both males and females do not appear to survive the third winter, while in 1950, even by the end of October, they had almost disappeared from the catch.

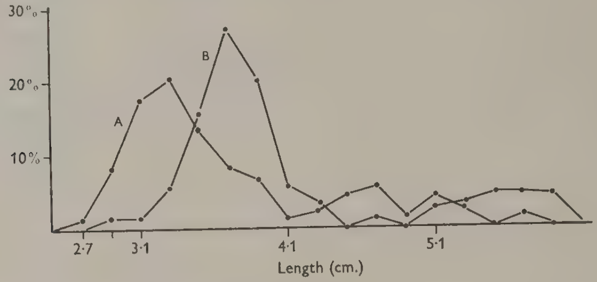

Fig. 5. Comparison of catches from: A, Trevol, 11 November (79); B, Paignton, 21 November (70).

## FOOD

A table of the stomach contents of *L. squilla* appears in the paper on *L. serratus* (Forster, 1951, p. 356). Like *L. serratus* the species is also omnivorous, though in the summer, as the table shows, it seems to select a considerable amount of filamentous algae, especially *Pylaiella littoralis* (kindly identified by Dr M. Parke). In the autumn, however, many crustaceans were also sometimes taken.

Although they did not appear in the stomachs examined, it seems probable that both cypris and nauplius barnacle larvae might commonly be taken in the spring. On one occasion a number of *Leander squilla* in a tank were observed behaving in a peculiar fashion, swimming up to the surface and hovering upside down underneath the surface film. Closer examination showed that they were feeding vigorously on several small swarms of nauplii which had originated from a few large specimens of *Balanus porcatus* attached to a stone on the tank.

## SUMMARY

The habitat preferences of *Leander squilla* in the Plymouth area are briefly discussed. Length measurements were taken over a period of 12 months to compare the growth and breeding biology in this area with Sweden.

The 1949 year group grew to a considerably larger average size in October than did the 1950 year group in the corresponding period. The average sea surface temperature was approximately 1·7° C. higher in 1949 and the air temperature about 2·74° C. higher. A more reasonable growth characteristic

was derived by using the mean temperature of the air rather than that of the sea surface, a result consistent with the fact that the species inhabits the upper shore pools.

The O-group males did not move up the estuaries so that the percentage of males was always higher in the Sound. This difference in behaviour, well known in *Crangon vulgaris*, is discussed in relation to the sex ratios found by Höglund (1943).

In contrast with Sweden, growth continued during the winter at Plymouth, and the maximum length attained was slightly higher.

The stomach contents showed a varied diet but with a predominance of filamentous algae.

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# OBSERVATIONS ON *NEPHROPS NORVEGICUS* (L.) AND ON AN EPIZOIC POPULATION OF *BALANUS CRENATUS* BRUG.

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(Text-figs. 1–4)

The Dublin Prawn or Norway Lobster, *Nephrops norvegicus* (L.), is widely distributed on soft muddy bottoms, usually between 10 and 50 fathoms. It is found as far north as Iceland and the North Cape, is common in the North Sea and off the Atlantic shores of the British Isles, and extends as far south as the coast of Morocco; a variety, v. *meridionalis* (Zariquiey-Cenarro, 1935) is found in the Mediterranean and Adriatic (see Havinga, 1929, and Heldt & Heldt, 1931, for details of its distribution). Some aspects of the general biology of *Nephrops* have been dealt with by Höglund (1942) and Poulsen (1946) for Scandinavian waters, and by McIntosh (1904, 1908) and Storrow (1912) for the waters off north-east England. To a large extent all these workers relied on market catches.

In the Clyde Area, where *Nephrops* is found in very considerable quantities at certain times of the year, a number of collections has been made, and information concerning the size, sex and presence of females in berry has been obtained. In addition, having repeatedly observed the presence of epizoic barnacles (*Balanus crenatus* Brug.) on many of the prawns, it was thought that observations on these might help, not only to interpret the prawn data, particularly with regard to the time and frequency of moulting, but in addition might give some information on the growth of barnacles under these rather unusual conditions.

## THE METHODS AND MATERIAL

The hauls were taken with a V.D. trawl (see Barnes & Bagenal, 1951, for details) on grounds off the Island of Bute and off Knock Castle (full Kilometre National Grid References 26/1159–1162 and 26/1763–1767). The first collection (June 1950) was taken from the former ground, and the later ones (July, August, October 1950 and January 1951) from the latter ground at a depth of 20 fathoms, where the prawn was found to be more plentiful. Supplementary hauls were taken in these and other places and will be referred to where appropriate.

All the prawns were measured from the point of the rostrum to the telson, to the nearest half centimetre below, and the sex and presence of berried females noted. At the same time, the small numbers of barnacles on telson, abdomen and cephalothorax were noted. The chelipeds which bore most of the epizoic barnacles were then removed and all the barnacles measured (carino-rostral length, using an eyepiece micrometer) and their distribution on the various parts of the chelipeds, namely meropodite, carpopodite, propodite and dactylopodite together, noted. In all, some 1200 *Nephrops* and 8000 barnacles have been examined and measured.

## THE GROWTH RATE OF *BALANUS CRENATUS* ON *NEPHROPS NORVEGICUS*

In the Firth of Clyde *Balanus crenatus* liberates nauplii throughout most of the year except for the winter months, but the major liberation and subsequent settlement takes place in the spring followed by a moderate liberation and settlement in August (Pyefinch, 1948).

TABLE I. THE ESTIMATED MEAN SIZES (MM.) OF *BALANUS CRENATUS* POPULATIONS ON *NEPHROPS* OBTAINED FROM SIZE-FREQUENCIES AND ANALYSES BY CUMULATIVE PERCENTAGES: EACH SIZE-GROUP OF *NEPHROPS* ANALYSED SEPARATELY AND THE RANGE OF MEANS GIVEN.

| | Population I | | Population II | | Population III | | Population IV | |
|---|---|---|---|---|---|---|---|---|
| Collection | Range of means | Grand mean | Range of means | Grand mean | Range of means | Grand mean | Range of means | Grand mean |
| June 1950 | 1·3–1·6 | 1·5 | 4·0–4·3 | 4·1 | 8·1* | 8·1 | — | — |
| July 1950 | 1·5–2·1 | 1·8 | 4·5–4·9 | 4·7 | 8·5* | 8·5 | — | — |
| August 1950 | 1·7–3·2 | 2·5 | 3·4–5·7 | 4·9 | — | — | — | — |
| October 1950 | 4·2–5·1 | 4·4 | — | — | — | — | 0·5–1·4 | 0·7 |
| January 1951 | 4·4* | 4·4 | — | — | — | — | 1·8* | 1·8 |

* Insufficient numbers to consider size-groups separately.

Size-frequency curves for the barnacles on each centimetre size-group of *Nephrops* have been drawn and analysed, and it has been found that in each collection of *Nephrops* similar barnacle populations were present irrespective of the size-group of the prawn (see later for exceptions and further discussion). In considering the barnacle populations all those collected on a given date are therefore considered together. The range of the estimated mean size from the various *Nephrops* size-groups and the estimated grand mean for these barnacle populations are shown in Table I. They are also plotted in Fig. 1, from which the following construction regarding the settlement and growth of these barnacles is put forward.

During the sampling period, from June to January, four populations (I–IV) of barnacles were found. The large individuals (mean 8·1 mm.) of population III were represented only in the June and July samples and then only as a very small fraction (*c.* 10%) of the whole barnacle population; population IV (small individuals, mean 0·7 mm.) was present only in the October and January samples and in the latter as a moderate proportion (*c.* 20%) of the whole. It seems clear from Fig. 1 that the growth-curve of population I is that of the spring settlement 1950, since extrapolation indicates its origin during the heavy April settlement. The growth-curve of population IV would seem to correspond to the moderate August settlement noted by Pyefinch (1948). The mean growth-rate in population I was uniform throughout the summer but fell off during the winter (see Pyefinch), whereas in population IV little growth took place before the winter and there was only a small increase in size between October and January. Allowing for this reduced growth rate during the winter and plotting the values as a hypothetical second year, with 'normal' growth rate established for populations I and IV in the following spring, it seems clear that the spring population of one year gives rise to the third (III) population observed in the spring of the next year; thus the extended curve I is equivalent to two seasons' growth of a spring settlement, so that population III, observed in June and July 1950, is the spring settlement of 1949. The autumn settlement becomes the medium-sized population II (extended curve IV) during the year after settlement; it is smaller since it has had only one period of maximum growth-rate, namely during the spring of its second year. The growth-curve of population IV thus gives rise in the second year to the curve of population II. To these is added the spring settlement in the second year.

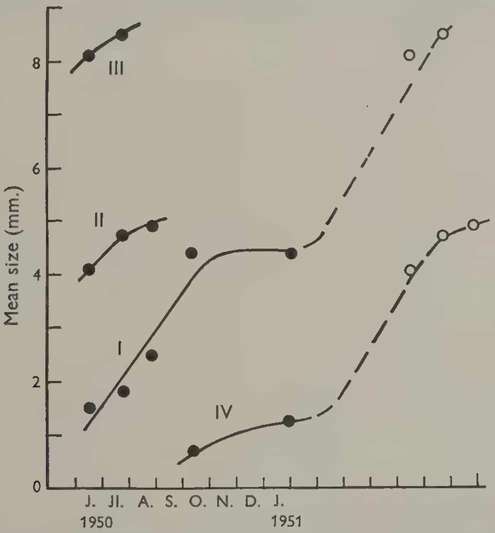

Fig. 1. The mean size of the *Balanus crenatus* populations. I, spat of spring 1950; II, spat of autumn 1949; III, spat of spring 1949; IV, spat of autumn 1950. ——, present year (1950). -----, next year (hypothetical).

On this hypothesis the growth-rates of the spring settlement during the summer months of its first year and also of the settlement of the previous autumn in its second year are very similar, about 2 mm. in 4 months. This is in marked contrast with the growth-rate of *Balanus crenatus* on raft-exposed panels, for which Pyefinch gives up to 0·2 mm. per *day*: it is more comparable with the value given by Topsent (1911) of 5–6 mm. in 3½ months for *B. crenatus* growing on the shore. Other observations have confirmed the high growth-rate on raft-exposed panels, and it would seem that the extremely slow growth-rate of the barnacles settled on *Nephrops* is largely due to the habitat of the prawn since, as Crisp (1951) has pointed out, the growth-rate of barnacles varies enormously in different environments. He finds that growth is greatest in clean water and high currents, while in slow currents, and particularly in the presence of much silt, it is considerably reduced. The latter conditions are, of course, just those which appertain to barnacles epizoic on *Nephrops*.

The above results emphasize the necessity of caution in the use of epizoic fauna as evidence regarding the age of the 'host' (as used, for example, by Foxon, 1940). For *Balanus crenatus* at any rate, and probably other species, only measurements of individuals growing under comparable conditions should be used.

A feature of interest not evident from the discussion may be mentioned. The enormous settlement of *B. crenatus* in 1950 resulted in material such as stones, shells or debris from the sublittoral zone usually being completely covered with living barnacles during the late spring and early summer. By late summer, although large quantities of calcareous remains were left on such material, living barnacles were comparatively few; indeed the whole population had been decimated. In contrast, all the barnacles examined from the *Nephrops* were living. The barnacles on the *Nephrops* may have owed their survival to a 'protective' action of the prawn, or perhaps to the absence of the predators in the muddy bottom habitat of *Nephrops*.

## THE MOULTING OF THE *NEPHROPS*

The population of large barnacles (III) was confined to two size-groups of *Nephrops*, 17–18 and 20–21 cm., in the first two collections of June and July (populations I and II being also present), and there were four other examples of a single barnacle population on a given size-group. Apart from these exceptions all the *Nephrops* size-groups at any given date had the same barnacle populations (twenty-five sets in all). It should, of course, be remembered that some *Nephrops* of each size-group were barnacle-free at any time. This suggests that moulting usually takes place irrespective of size-group; at no time did a given *Nephrops* size-group lose all its epizoic barnacles, or carry a distinctive barnacle population. Now it may be seen from Fig. 1 that, on the hypothesis put forward in the previous section, the spring barnacle settlement of one year is lost by August of the next year (population III, although present in small numbers—2% of the total—in July was absent in August) and further, the summer settlement of one year is lost by the autumn of the next year (population II, although present up to August, was absent in October). The life of a barnacle on a prawn does not exceed one year. This suggests that in any size-group a *Nephrops* moults at least once a year. It cannot be ascertained from these results whether any given prawn moults more frequently, but few individuals appear to moult less than once a year, at any rate not enough to contribute a detectable population of barnacles to that carried by a given size-group. It may be objected that the barnacles themselves do not live after the first year; this, however, would seem unlikely, since *Balanus crenatus* is known to live for much longer periods in its normal habitat, and, further, had this been so, their calcareous bases would have been left and observed.

TABLE II. PERCENTAGE OF *NEPHROPS* WITH EPIZOIC *BALANUS CRENATUS*

| Size group (cm.) | June | July | August | October | January |
|---|---|---|---|---|---|
| 7–8 | 0 | 0 | 0 | 0 | — |
| 8–9 | 0 | 0 | 0 | 0 | — |
| 9–10 | 0 | 0 | 0 | 0 | — |
| 10–11 | 0 | 0 | 0 | 0 | 0 |
| 11–12 | 0 | 0 | 0 | 0 | — |
| 12–13 | 51 | 6 | 13 | 0 | — |
| 13–14 | 31 | 10 | 9 | — | — |
| 14–15 | 50 | 13 | 19 | 57 | 0 |
| 15–16 | 43 | 24 | 41 | 64 | 0 |
| 16–17 | 75 | 37 | 38 | 83 | (66) |
| 17–18 | 79 | 57 | 46 | 81 | 56 |
| 18–19 | 89 | 45 | 58 | 83 | 50 |
| 19–20 | 100 | 51 | 76 | 88 | 92 |
| 20–21 | 100 | 35 | (100)* | 79 | 86 |
| 21–22 | 100 | 43 | — | 100 | (100) |

* A bracketed value signifies only very small number ($<10$) of individuals.

The above results indicate that some moulting takes place in the late spring and also in the early autumn. Table II gives the percentages, at each collection, of the *Nephrops* in the various size-groups with barnacles (for a consideration of the barnacle-free size-groups see p. 377), and the drop in these percentages between the June and July collections indicates that some moulting also took place at this time. There is little change in these percentages in August, and the increase in October is presumably due to the moderate barnacle settlement in August. The numbers of *Nephrops* in the January collection were small, and the values are therefore less reliable, but the decrease in the 17–19 cm. size-groups may be due to moulting or perhaps mortality of the smaller barnacles during the winter months. Storrow (1912) found that soft or 'recovering' males were found mainly in the spring catches (April), but some were present throughout the year except in the late autumn and early winter (September–November).

### Maturity and Breeding Season of *Nephrops*

In all these collections only seventy-eight female *Nephrops* have been taken, compared with 1200 males, and on no occasion were the females ever more than 9% of the catch (Table III): Poulsen gives the proportion of females in his material as about 30%. In the Scandinavian material berried females were found in all the size-groups greater than 12 cm., but Havinga (1929) gives the size at sexual maturity, presumably for material in more southerly regions, as 10 cm., with rare individuals at 8 and 9 cm. Storrow (1912, 1913) records berried females at 9–11 cm. but the majority were in the size-groups greater than 11 cm. Most of the berried females collected in the supplementary hauls in this region were in the size-groups of 10 cm. and above, but a small number have been found berried at 7·5 cm.

Table III. Size-Frequency (nos.) Distribution of Female *Nephrops*

| Size group (cm.) | June | July | August | October | January |
|---|---|---|---|---|---|
| 8–9 | 0 | 1 | 2 | 0 | Nil, but very small catches |
| 9–10 | 1 | 2 | 5 | 0 | |
| 10–11 | 0 | 10 | 10 | 1 | |
| 11–12 | 5 | 11 | 6 | 2 | |
| 12–13 | 1 | 8 | 3 | 1 | |
| 13–14 | 3 | 0 | 1 | 1 | |
| 14–15 | 1 | 1 | 0 | 2 | |
| Total | 11 | 33 | 27 | 7 | — |
| Berried | 0 | 0 | 2 | 0 | — |
| Percentage of total catch | 8·0 | 5·6 | 8·8 | 3·4 | — |

Berried females have been taken from August to January, and in all these eggs were in the unripe green state. This is in agreement with Storrow's observation that spawning takes place from July to September and, according to this worker, the female carries the eggs for a long period, and then hatching takes place in the following spring and summer. It would seem that the spawning and hatching take place somewhat later than in Scandinavian waters (see Poulsen, 1946).

Poulsen has suggested that the fact that the percentage of berried females sometimes approaches 50% of the adult female population indicates a biennial spawning, and that any reduction below this value is due to the berried females burrowing more deeply. There seems little evidence to support the view that the females in general burrow more deeply (see p. 377), and the very small proportion of berried females recorded here and also by Storrow would indicate a very infrequent spawning. An alternative possibility is that the females, after fertilization, tend to migrate away from the grounds usually fished, for Meek (1903, 1913, 1914) has suggested that the well-known migration of crabs is related to the ripening of ova: it seems clear from his work that female crabs migrate far more readily than males. In Meek's work the percentage of female *Nephrops* dropped from June-August and this would agree with fertilization in late spring and subsequent migration.

## THE SIZE AND SEX RATIO OF *NEPHROPS*

The frequency of the various size-groups is given in Tables III and IV, and for the males the appropriate histograms have been drawn in Fig. 2. The range in size both for males and females, 7–24 and 7–15 cm., respectively, is similar to that given by both Poulsen and Storrow, although the former records occasional males as large as 25 cm., while the latter's records do not show any larger than 22 cm. (The lower size limit is, of course, determined in part by the trawl-mesh size used).

TABLE IV. PERCENTAGE-SIZE-FREQUENCY OF ALL THE MALE *NEPHROPS* COLLECTED

| Size group (cm.) | June | July | August | October | January |
|---|---|---|---|---|---|
| 6–7 | 0·0 | 0·0 | 0·4 | 0·0 | 0·0 |
| 7–8 | 0·7 | 0·2 | 0·0 | 0·0 | 0·0 |
| 8–9 | 0·7 | 0·6 | 0·4 | 0·5 | 0·0 |
| 9–10 | 0·7 | 1·3 | 2·8 | 0·5 | 0·0 |
| 10–11 | 2·9 | 3·1 | 6·0 | 2·0 | 2·6 |
| 11–12 | 5·8 | 3·2 | 5·2 | 1·5 | 7·7 |
| 12–13 | 9·5 | 3·1 | 6·4 | 1·5 | 0·0 |
| 13–14 | 11·7 | 7·8 | 9·2 | 0·0 | 0·0 |
| 14–15 | 13·1 | 6·7 | 12·4 | 7·0 | 2·6 |
| 15–16 | 5·1 | 14·5 | 10·8 | 5·5 | 2·6 |
| 16–17 | 8·8 | 17·0 | 13·6 | 17·6 | 7·7 |
| 17–18 | 17·5 | 15·4 | 9·6 | 16·1 | 0·0 |
| 18–19 | 13·1 | 11·4 | 9·6 | 17·6 | 20·5 |
| 19–20 | 5·8 | 7·8 | 12·0 | 17·6 | 20·5 |
| 20–21 | 2·2 | 4·4 | 1·2 | 9·6 | 25·6 |
| 21–22 | 1·5 | 1·3 | 0·0 | 2·0 | 10·3 |
| 22–23 | 0·0 | 0·2 | 0·0 | 1·0 | 0·0 |
| 23–24 | 0·7 | 0·2 | 0·4 | 0·0 | 0·0 |

There is no separation into distinct year-classes, but unlike Poulsen's data there is an indication of an increase in the proportion of the larger size-groups throughout the season. The reason for this difference is not entirely clear. Both Poulsen's and Storrow's data were obtained from material obtained over a wide area, or from market catches, while the present catches were always taken in the same place. The simplest explanation would be to assume that differential changes took place (as a result of migrations) with respect to size-groups in the present collections which were taken in one locality, and that this resulted in an accumulation of the larger size-groups in the area sampled.

In these and all other records the great proportion of males in all the catches and at all times of the year has been stressed. Poulsen has suggested that this is due to the females burrowing more deeply, and therefore being less likely to be taken in a trawl. The explanation seems hardly adequate; although the smaller animals may, as is suggested later (p. 377) lead a more secluded life, and may therefore be inadequately represented in the catches; an examination of the numbers for the smaller size-groups shows that the males and females are caught in roughly equal numbers (Table V): this is also seen in the figures given by Poulsen (1946), Storrow (1912, 1913) and McIntosh (1904). The inequality in the sex ratio only becomes apparent when the large size-groups are considered.

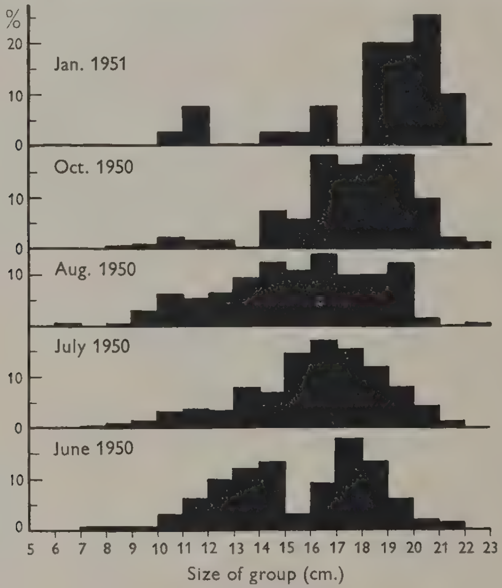

Fig. 2. Size-frequency histograms of *Nephrops* (collections I–V).

TABLE V. SIZE-FREQUENCY (NOS.) OF MALE AND FEMALE *NEPHROPS* FOR 7–15 CM. GROUPS

| Size group (cm.) | June | | July | | August | | October | |
|---|---|---|---|---|---|---|---|---|
| | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 7–8 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| 8–9 | 1 | 0 | 1 | 1 | 0 | 4 | 0 | 0 |
| 9–10 | 1 | 1 | 5 | 6 | 5 | 5 | 0 | 0 |
| 10–11 | 3 | 0 | 11 | 11 | 9 | 9 | 1 | 1 |
| 11–12 | 4 | 5 | 18 | 18 | 12 | 8 | 1 | 2 |
| 12–13 | 14 | 1 | 15 | 11 | 12 | 3 | 0 | 1 |
| 13–14 | 14 | 3 | 25 | 2 | 7 | 1 | 3 | 1 |
| 14–15 | 14 | 1 | 40 | 0 | 9 | 1 | 0 | 0 |

The above facts, together with the smaller size-range of the females, suggests that the sexes are present in the same number up to 12 cm., but beyond this size there is differential mortality—the females living little longer than the time required to reach sexual maturity, while the males continue to grow for some years (contrast Punnett, 1904).

### THE HABITAT OF *NEPHROPS* AND THE BARNACLE SETTLEMENT

Poulsen remarks that it is well known that adult *Nephrops* hide in the bottom mud and that this has not been demonstrated for the younger individuals. It has now been shown that these young individuals do indeed burrow in the mud. Fig. 3 is a photograph of a burrow of a 5 cm. *Nephrops* kept on mud in a tank; the burrow was 10–12 cm. in length, shallow and open at both ends, and sufficiently long to hide the entire animal (including chelipeds) which indeed had retracted into the burrow before the photograph was taken. Although larger *Nephrops* have not been seen to make burrows in laboratory experiments it seems unlikely that a burrow proportional in length could readily be maintained in soft mud: this would require a burrow 60 cm. long for a 24 cm. *Nephrops*.

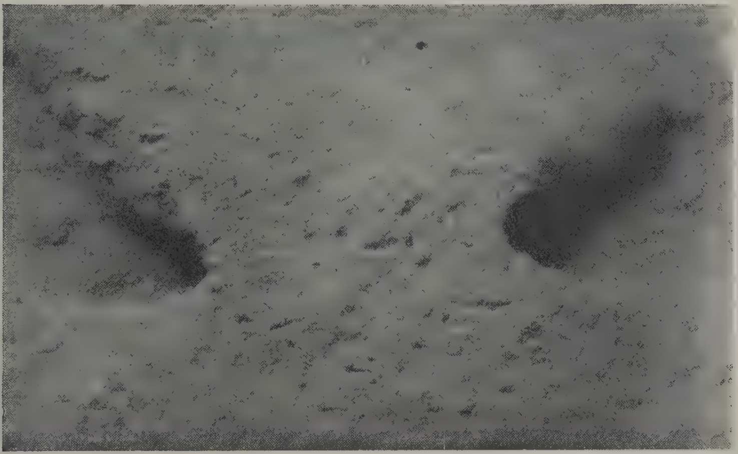

Fig. 3. Burrow made by a 5 cm. *Nephrops* kept on mud in an aquarium tank. Length of burrow 10–12 cm., with entrance on the left and the *Nephrops* completely hidden. × 0·7.

The above observations suggest that the smaller animals, males and females, may lead a more secluded life than the larger ones and this is borne out by the fact that all the *Nephrops* up to 11 cm. were completely free from barnacles, although it must be remembered that the larger individuals present a larger surface area for settlement.

The distribution of barnacles on these larger *Nephrops* is illustrated in Table VI and Fig. 4, and these results suggest quite clearly that the animals spend much of their time in their relatively smaller burrows, with the thorax just protruding and the heavy chelipeds resting with their lower surfaces on the mud.

TABLE VI. DISTRIBUTION OF BARNACLES (ALL SIZES), JULY COLLECTION

| | *Nephrops* with barnacles (%) | Total barnacles present (%) |
|---|---|---|
| Cephalothorax | 12 | 3·5 |
| Meropodite | 5 | 1·2 |
| Carpopodite | 41 | 18·4 |
| Pro- + dactylopodite | 74 | 76·6 |
| Telson | 1 | 0·1 |
| Abdomen | — | 0·3 |

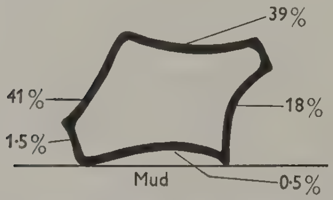

Fig. 4. Diagrammatic cross-section of the right propodite of *Nephrops*, showing the percentage distribution of barnacles on the various regions for the July collection.

## SUMMARY

Data have been given concerning the size-frequencies, sex and presence of females in berry of *Nephrops norvegicus* in the Clyde Sea Area, and also the numbers, size and distribution of *Balanus crenatus* epizoic on the prawns. This entailed the examination of *c.* 1200 *Nephrops* and *c.* 8000 barnacles, taken in June, July, August and October 1950 and January 1951.

Four barnacle populations were found during the sampling period, and these have been shown to originate from two periods of settlement (April and August).

The growth-rates of the spring barnacle spat-fall during its first summer, and the settlement of the previous autumn in its second year, are both shown to be about 2 mm. in 4 months, and reasons for, and consequences of, this slow growth-rate are put forward.

It is suggested from the evidence provided by the examination of epizoic barnacles on the prawns that the moulting of the latter takes place irrespective of the size-group, at least annually and largely between late spring and early autumn.

Females may attain sexual maturity (as evidenced by the carrying of eggs) at 7·5 cm., but the 10 cm. size-group is more commonly mature. Berried females are observed between August and January.

Size-frequency histograms are given for the males, and the shift in the population towards the higher size-groups is tentatively explained on the basis of differential migration.

It is pointed out that the differences in proportion of males and females is only evident when the higher size-groups are included; below 12 cm. the numbers for both sexes are similar for these and other observations. The suggestion that the females burrow more deeply is therefore open to question.

It is shown by laboratory experiments that young *Nephrops* are able to construct burrows 2½ times their length; the entire absence of barnacles on prawns of less than 11 cm. is correlated with the ability of these smaller animals to become completely hidden. The distribution of *Balanus crenatus* on the larger *Nephrops* suggests that these also live in the mud but that the burrows are not proportionately as large; they spend much of their time at the entrance of their relatively smaller burrows with the heavy chelipeds resting on the mud surface.

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# THE GROWTH-RATE OF JUVENILE *ASTERIAS RUBENS* L.

By H. Barnes and H. T. Powell

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(Text-fig. 1)

The general biology of the common starfish, *Asterias rubens* L., has recently been studied by Vevers (1949), whose investigations included observations on the growth-rate of this species. His material was collected in the Plymouth area largely by means of an otter trawl, supplemented by a few Agassiz and dredge hauls, and there are therefore few records in his data of the growth-rate of juvenile *A. rubens* under natural conditions. Vevers also made observations on the growth-rate of individuals kept in laboratory tanks, but again the results apply mainly to fairly large animals. The only other direct observations on growth-rate appear to be those of Bull (1934), who dealt with three small individuals kept in aquarium tanks, while Orton & Fraser (1930) give measurements made on a natural population taken, after one year's growth, from a buoy.

While examining barnacle-covered panels, suspended 2 ft. below the surface from a raft moored at Millport, large numbers of very small (about 4·5 mm. radius) *A. rubens* were noted during early August 1950 and, in view of the lack of information on the growth-rate of such small starfish, samples of this population were collected and measured at intervals over a period of 6 months; the data so obtained supplement those given in the investigations referred to above.

The panels (each 15 × 10 in.) had only been exposed since March 1950 and by the beginning of August, when the collections of starfish were first made, were covered with close-packed elongated barnacles—mixed *Balanus crenatus* Brug. and *B. balanoides* (L.), similar to the growth described and figured by Barnes & Powell (1950, Pl. I)—together with numerous young *Mytilus edulis* L. Although many of the barnacles had already been killed by the predatory activities of the nudibranch *Onchidoris fusca* (O. F. Müller), large numbers of which were present on the panels at this time, the panels would appear from the point of view of food supply to have been an ideal site for the growth of young starfish.

There were a number of such panels all carrying this young *Asterias* population, and each subsequent sample of the latter consisted of all the starfish that could be found on one or more of the densely colonized panels. No panel was sampled more than once, errors due to selection being thereby minimized. The animals were brought into the laboratory and killed in weak alcohol with the arms fully extended, and measured immediately. In view of the difficulty of determining the exact position of the anus in the smallest specimens, the distance from the centre of the disk to the tip of the longest ray was measured and this measurement was adhered to in all subsequent samples; a vernier measuring microscope was used for the smaller, and ordinary dividers for the larger animals. Table I gives the dates of collection, the numbers of starfish measured, the mean length (radius), the standard error of each mean, together with the increase in the mean length per 30 days. The mean lengths and the monthly mean surface sea-water temperatures near the site are plotted in Fig. 1.

In the subsequent discussion of growth-rate our results can be considered comparable with those of Bull (1934), who gives the mean radius of all the arms of normal length of each individual measured from the centre of the disk, and with those of Vevers, although the latter author in accordance with general convention for adult asteroids, measured the distance from the anus to the tip of the longest arm. In considering the results of Orton & Fraser (1930), the conversions made by Vevers are used.

It is well known that large starfish wander over considerable distances, and they may climb on to rafts and moored buoys via the mooring chains. It is considered that the population under consideration, which was under observation at frequent intervals (in addition to the occasions when the starfish samples were being taken) received no influx in this way. The possibility exists that some of the larger starfish may have dropped off the panels but this is considered unlikely, although late in the season there was some evidence that the larger starfish did move from panel to panel. It is almost certain that the young starfish had developed from larvae which settled directly on the panels since, according to Gemmill (1914), spawning of *A. rubens* takes place at Millport from April to June, varying somewhat from year to year, and development of the larva to the youngest adult form takes from 9 to 10 weeks.

Irregularities in the growth-rate curves of *A. rubens* seem to be common, as is emphasized by Vevers in discussing his results; a similar irregularity is seen in our growth-curve which is that of mean sizes. However, there were two periods of uniform growth: in the first period (7 August 1950 to 5 October 1950) the average of the separate estimates of the rate of increase of the mean size is 4·4 mm. per 30 days, while in the second period (2 November 1950 to 22 January 1951) the value is somewhat lower: 3·2 mm. per 30 days (see Table I and Fig. 1).

Vevers (1949, p. 172) points out that starfish up to at least 6 cm. radius can grow at a monthly rate of rather more than 10 mm. in the summer and rather less than 5 mm. in winter. However, his two smallest animals, B 8 and B 9, show the variation in growth which can take place between individuals kept under apparently identical environmental conditions. Thus B8 grew from 13 to 39 mm. from 6 July to 21 September 1947, that is an overall rate of 10 mm.

TABLE I. ANALYSIS OF GROWTH-RATE OF SAMPLES OF YOUNG *ASTERIAS RUBENS*

| Date of collection | No. in sample | Mean length (*r*) of sample (mm.) | Standard error | Increase in mean length (*r*), mm. per 30 days |
|---|---|---|---|---|
| 7 Aug. 1950 | 33 | 4·6 | 0·39 | 3·3 |
| 19 Aug. 1950 | 31 | 5·9 | 0·33 | 4·4 |
| 30 Aug. 1950 | 48 | 7·5 | 0·29 | 5·5 |
| 16 Sept. 1950 | 38 | 10·6 | 0·47 | 4·4 |
| 5 Oct. 1950 | 50 | 13·4 | 0·66 | 10·4 |
| 18 Oct. 1950 | 71 | 17·9 | 0·58 | 2·0 |
| 2 Nov. 1950 | 75 | 18·9 | 0·56 | 3·8 |
| 5 Dec. 1950 | 73 | 23·1 | 0·64 | 2·9 |
| 28 Dec. 1950 | 68 | 25·3 | 0·71 | 3·0 |
| 22 Jan. 1951 | 78 | 27·8 | 0·97 | |

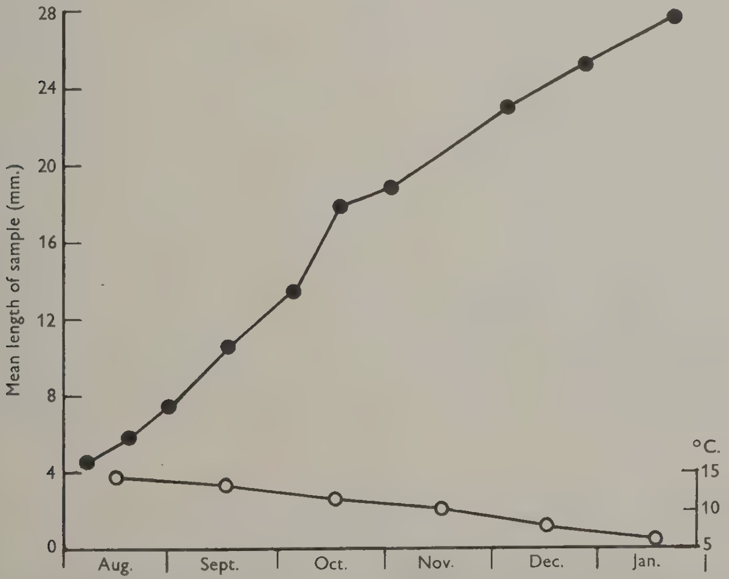

Fig. 1. The mean length (*r*) of samples of a population of *Asterias rubens* growing on raft-exposed panels (●), together with the monthly mean surface sea-water temperatures near the site (○).

per 30 days, and B9 increased from 10 to 27 mm. during roughly the same period (20 July to 21 September 1947), an overall rate of 8·1 mm. per 30 days. The latter animal (B9) increased its overall rate to 11 mm. per 30 days during the late autumn and winter (26 October to 14 December 1947).

The present results are for the means of a series of samples, and therefore supply no information regarding variation in growth-rate of individuals of the same age or size, but in view of the variations discussed above there would not seem to be any great discrepancy between our results and those of Vevers, although in general the latter are somewhat greater; indeed he estimated that the animals used in his experiments had grown at an average rate of 5 mm. per month over the 12 months before capture.

The results are also in agreement with those of Bull (1934) for the growth of two of his animals, 2(*b*) and 3, reared in the laboratory; these showed an overall growth rate of 3·3 and 6·0 mm. per 30 days respectively during comparable periods of the summer and early autumn months (May to September 1929).

Orton & Fraser (1930) measured 1805 small *A. rubens* taken from a buoy in Liverpool Bay, and estimated that the modal size attained by this population after 1 year's growth was 22 mm., with a range from 6 to 52 mm.; this corresponds to a monthly increment of approximately 2·5 mm. around the mode (which was little different from the mean). The growth of this population, therefore, was much less than that observed either in the experimental animals of Bull and Vevers or in those of the present investigation.

Vevers's results have clearly shown the great effect of reduced food supply in lowering the growth-rate of animals of such voracious habits as *A. rubens*. Both his and Bull's animals were reared in laboratory tanks with a plentiful supply of the appropriate kind and size of food, and the present results show that a similar growth-rate can be attained under natural conditions. The discrepancy between these results and those of Orton & Fraser would hardly seem to be due to a temperature effect, since the surface seawater temperatures at Millport (Fig. 1) are very similar to those of Liverpool Bay (Proudman, Lewis & Dennis, 1937). It is considered that a shortage of food of the appropriate kind at some stage in their growth, rather than possible loss of some of the larger animals due to wind and wave action, is more likely to account for this discrepancy.

## SUMMARY

A population of young *Asterias rubens* settled on raft-exposed panels has been sampled at frequent intervals over a period of 6 months.

The conditions under which this population developed are described, and from the measurements obtained estimates are given of the growth-rate during the period of the observations.

These values are compared with those obtained by other workers.

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# OBSERVATIONS ON *SPHENIA BINGHAMI* TURTON

By C. M. Yonge, F.R.S.

From the Department of Zoology, University of Glasgow

(Text-figs. 1, 2)

The family Myidae is represented in British seas by the two large and well-known species, *Mya arenaria* L. and *M. truncata* L., which burrow deeply into muddy sand and into stiff mud or clay respectively, and by the much smaller *Sphenia binghami* Turton. Interest in members of this family of Eulamellibranchia was aroused during 1949 when studying two species which are common along the coast of California, namely *Platyodon cancellatus* (Conrad) and *Cryptomya californica* (Conrad). These differ most interestingly in habitat. The former bores into soft rocks between tide marks, and the latter, although practically devoid of siphons, burrows deep in the mud of tidal estuaries, always in association with burrows made by various large invertebrates. The species most usually involved is *Callianassa californiensis*, a large anomuran prawn (McGinitie, 1935). The almost sessile siphons open into the sides of the burrows. Accounts of both species have been prepared for publication in California.

The desire to survey more widely the range of form and habit in this family led to this inquiry into *Sphenia binghami*. This has been described and also figured, although indifferently, by Forbes & Hanley (1853) and Jeffreys (1865). They record a wide distribution in depths of between 5 and 25 fathoms in the Mediterranean, along the Atlantic coasts of Spain and France, and around the British Isles as far north as Scarborough on the east and Skye on the west. But there is a surprising paucity of recent records, and certainly during the present century this species has been almost completely overlooked. By the kindness of Dr W. J. Rees, shells collected off Weymouth by Canon A. M. Norman and now in the possession of the British Museum (Natural History) were examined. But no complete specimens were available. *S. binghami* is not listed in the Plymouth Marine Fauna (Marine Biological Association, 1931), although it very probably occurs in that area. There are a number of early records from the Clyde sea area but no specimens have as yet been found in the course of the faunal survey at present being conducted from Millport. Dr H. O. Bull states that it is not recorded from the Cullercoats area. It is, however, listed in the Marine Fauna of the Isle of Man as occurring in various localities around the island at depths of between 12 and 26 fathoms.

Specimens were finally obtained from the marine station at Port Erin through the kindness of Dr N. Sumner Jones who identified them during the course of his work on the bottom fauna and sent them living, by air, to Glasgow. This work would have been impossible without his help and care.

## HABITAT

Some ten specimens were eventually received, the majority alive, the largest being only about 1 cm. long. Dr N. S. Jones writes saying that 'all the specimens I have found came from an area about one to two miles south of the Calf of Man, in about 20 fathoms. The bottom consists of gravel and fairly large stones, many of which are limestone. I picked out all the stones brought up in the dredge that showed holes bored by *Hiatella*. The *Sphenia* inhabit these holes, presumably after the death of the original occupant. I obtained them by breaking up the stones with a hammer and picking them out of the cavities. For each *Sphenia* there must have been about 50 living *Hiatella*.' The accounts given by Forbes & Hanley and by Jeffreys are very similar, the latter writing of the occurrence of *Sphenia* within cavities of limestone rocks and oyster shells perforated by *Saxicava rugosa* (*Hiatella rugosa*) and *Cliona celata* and also within the holdfasts of *Laminaria*.

There is no doubt that *Sphenia* has been overlooked for so long owing to confusion with the much commoner *Hiatella* with which it normally lives and which it superficially resembles. When the siphons are extended distinction between the species is easy, those of *Hiatella* being red and also relatively longer with the two openings the more widely separated. But when contracted only careful examination of the ligament, external in *Hiatella* and internal in *Sphenia*, provides certain indication. Both *Sphenia* and the two species of *Hiatella*, no matter whether the latter are boring or byssal-attached individuals (Hunter, 1949) are frequently very iregular in shape. Jeffreys refers to the frequent distortion of the shell in *Sphenia* and this was also noted in all the specimens personally examined, three of which are shown in Fig. 1. This irregular shape is certainly associated with the mode of life, namely attachment by byssus (see Fig. 1 B) within crevices, often those initially formed or else increased in size by *Hiatella*, in stones or shells. The lack of mobility and the nature of the habitat was further indicated by the presence of encrusting growths of hydroids, polyzoa, etc., both on the shell and on the periostracum at the base of the siphons.

## DESCRIPTION

*Shell*. This is white in colour and typically almost twice as long as broad, seldom much exceeding 1 cm. in length. It has been well described by Forbes & Hanley and by Jeffreys, and only points of special interest demand mention. The hinge is situated about one-third of the distance from the anterior end and possesses the chondrophore characteristic of the Myidae with the associated condensed internal ligament (Fig. 2, *l*). The asymmetry of the hinge mechanism is responsible, as in all Myidae, for the shell being inequivalve, the right valve being the larger as shown in Fig. 1, A–C. This asymmetry is still more marked in *Aloidis* (*Corbula*), a genus included with the Myidae in the Myacea (see Thiele, 1935). There is a slight posterior gape but the shell valves in this region as indicated in Fig. 1 A–C, are very weakly calcified, another point of resemblance with *Aloidis*, although calcified plates occur in this region in *A. gibba* (Yonge, 1946).

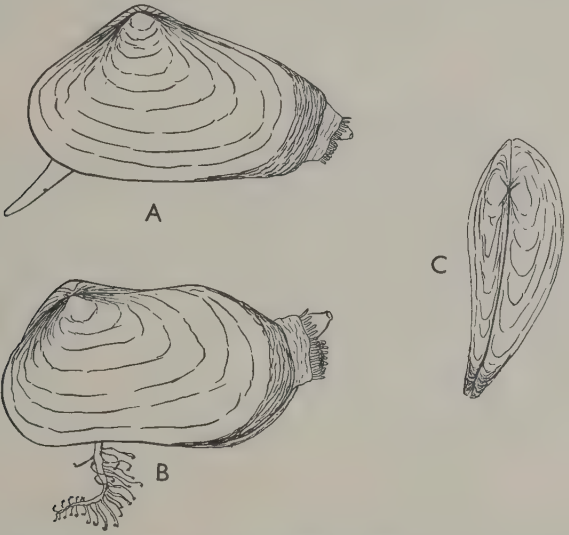

Fig. 1. *Sphenia binghami*, sketches of living specimens showing variation in form. A, specimen viewed from left side with foot and siphons projecting, × 10; B, specimen showing byssus, also siphons projecting, × 8; C, specimen viewed from dorsal aspect showing asymmetry of valves, right being the larger, and also twisting of the shell valves posteriorly due to environmental influences, × 4. In all the posterior area of uncalcified shell is indicated.

*Intact animal.* The only previous description of the living animal appears to be that furnished by Forbes & Hanley, and based on an account by a Mr Clark who observed the animal at Exmouth. It is substantially correct. As shown in Fig. 1 A, the small foot is thin and wedge-shaped, its prime function being to plant the stout byssus thread shown in Fig. 1 B. The short siphons are united and, as in Myidae generally, surrounded with periostracum. The siphons are thus composed of the inner and middle lobes of the mantle edge, together with the periostracal groove (Yonge, 1948). There is a common outer row of simple tentacles, numbering about 36 in a specimen of shell length 8·0 mm. The inhalant siphon is fringed with an inner row of tentacles, about 12 in number in the specimen mentioned above. These arch inwards, acting as strainers. The exhalant siphon has a tubular membrane which is very mobile. Although slightly longer, the siphons of *Sphenia* closely resemble those of *Aloidis gibba* (Yonge, 1946). But they are less sensitive, probably because there is much less danger of any sudden intake of sediment than in the mud-living *A. gibba*.

*Organs in the mantle cavity*. The appearance after removal of the left shell valve and mantle lobe is shown in Fig. 2. Owing to the greater portion of the shell being posterior to the hinge and umbo—associated presumably with byssal attachment—the anterior adductor (*ad*) is much smaller than the posterior adductor (*pd*) and is also displaced ventrally. The same is true of the anterior pedal retractor. The pedal gape is small, in correspondence with the small size of the foot, and the inner opening is bounded laterally by glandular areas (*g*), just as described in *Mya* (Vlès, 1909) and *Aloidis* (Yonge, 1946), and also present in *Cryptomya* and *Platyodon*. This appears to be a characteristic feature of the Myacea. Apart from the pedal gape the mantle edges are united ventrally, the inner and middle lobes being fused and also the periostracal grooves so that, as in the siphons, the mantle tissues exposed ventrally when the valves separate are everywhere covered with periostracum. But the mantle edges are not thickened as they are in the deep-burrowing *Mya arenaria* or *M. truncata* where, as previously suggested (Yonge, 1949), they probably assist in separating the shell valves. The gills, which are not plicated, are large, the inner demibranch being the larger but the outer one having a short supra-axial

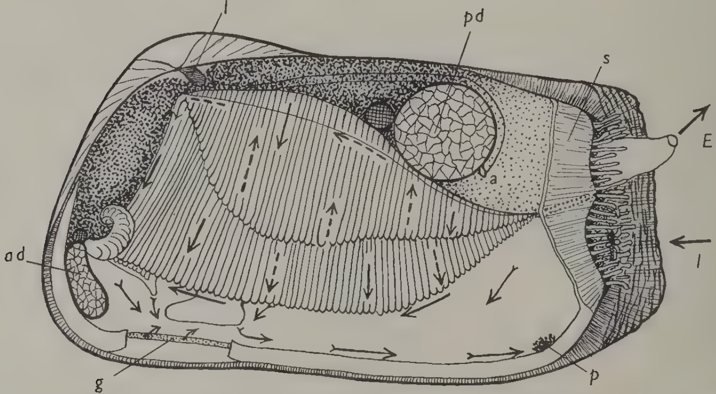

Fig. 2. *S. binghami*, animal viewed from left side after removal of left shell valve and mantle lobe, × 10. *a*, anus; *ad*, anterior adductor; *E*, *I*, exhalant and inhalant currents; *g*, glandular area; *l*, internal ligament; *p*, pseudofaeces; *pd* posterior adductor; *s*, base of siphons covered with periostracum. Complete arrows show currents on exposed surfaces on gills, broken arrows currents on under surfaces, feathered arrowas rejection currents.

extension. There is a food groove along the edge of the inner demibranch only. The palps are small but typical in form; they have few but relatively large ridges.

The only point of interest in the internal anatomy is the style which lies in a sac separated from the mid-gut as in all other Myidae (though not in *Aloidis*). It is stout and straight and can be seen through the translucent walls of the visceral mass in the intact animal after removal of the shell. It was observed to rotate at a speed of about 60 revolutions a minute.

*Ciliary currents*. The nature of these is indicated by the arrows on Fig. 2. Frontal cilia carry particles ventralward on the outer surface of the outer demibranch but dorsalward, to the axis, on the inner surface. Along the axis there is a weak forward current. Although there is no food groove along the ventral margin of the outer demibranch, and most particles are carried around it to the inner surface, there is some slight forward movement due probably to large cilia such as those described in *Aloidis* where the course of the ciliary currents is identical in other respects (Yonge, 1946). On the inner demibranch frontal cilia beat ventralward on both faces and particles are carried oralward in a marginal food groove. Particles on the mantle surface are conveyed ventrally and eventually accumulate at the posterior end as masses of pseudofaeces (*p*). The cilia on the glandular patches lateral to the pedal gape are especially dense and long, and beat away from the pedal gape; there are small vortices on either side of the posterior end of the pedal gape, although not as well developed as those in *Mya* (Kellogg, 1915; Yonge, 1923). This again indicates that the problem of removing excess material from the mantle cavity is much less in byssally attached bivalves living in clean water than in those that burrow in soft substrata.

## Discussion

*Sphenia binghami* is revealed as a member of the sublittoral fauna specialized for life at moderate depths under rather restricted conditions, but clearly less successfully than the two species of *Hiatella*, individuals of which are so very much the more common. The shell in *Sphenia* can certainly be modified to suit the constraint of the habitat while the foot, though doubtless capable of enabling the animal to move, is primarily concerned with planting the byssus. This mode of attachment is probably responsible, as in *Mytilus*, for the reduction of the anterior in relation to the posterior portion of the body. Unlike the other members of the Myidae, *Sphenia* is heteromyarian. The short siphons are adequate for the collection of suspended matter on which the animal feeds.

After publication of the accounts of *Cryptomya* and *Platyodon*, it is hoped to prepare a comparative account of the Myacea (i.e. the Myidae and also

*Aloidis*) showing how the basic form possessed by this group of Eulamellibranchia has been variously modified in connexion with specialization for life under a surprising variety of conditions.

## SUMMARY

*Sphenia binghami* Turton is a small member of the Myidae with the characteristic features of this family but adapted for life attached by a byssus within crevices in stones or shells at moderate depths. It is usually found with species of the much more numerous *Hiatella*. It has been confused with these, all having characteristically irregular shells. But examination of the ligament (internal in *Sphenia*, external in *Hiatella*) is enough to distinguish between them. Byssal attachment is probably responsible for the reduction of the anterior in relation to the posterior portion of the body and so for the heteromyarian condition not found in other genera of the Myidae.

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# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### Nitrogenous Excretion of Amphipods and Isopods

By **E. I. B. Dresel** and **V. Moyle**

*Journ. Exp. Biol.*, Vol. 27, 1950, pp. 210–25

The nitrogen excretion of eleven species of amphipods and isopods, including marine, fresh-water and terrestrial forms, has been studied. All species are essentially ammonotelic, since more than 50% of the total soluble non-protein nitrogen of the excreta was present in the form of ammonia throughout. The level of nitrogen excretion is appreciably lower in the terrestrial species than in any of the others, indicating that, in this group, adaptation to terrestrial conditions has been attended by a general suppression of nitrogen metabolism rather than by a transformation to other, less toxic products.

Some 5–10% of the total soluble non-protein nitrogen was present as urea in the case of the fresh-water amphipod, *Gammarus pulex*, and as uric acid in the terrestrial isopods as well as the fresh-water isopod, *Asellus aquaticus*. It is suggested that these minor excretory components might originate from purines as a result of the loss of one or more uricolytic enzymes. In association with the excretion of uric acid some retention of this compound usually occurs, and it was found that the amount so stored in the terrestrial species parallels the degree of morphological and physiological adaptation to terrestrial conditions. The greatest accumulation of uric acid was, however, observed in the fresh-water species, *A. aquaticus*, and although such a storage cannot necessarily be taken as evidence for a partially uricogenic metabolism, this possibility must be borne in mind. E.I.B.D. & V.M.

### The Effect of Stimulation on the Opacity of a Crustacean Nerve Trunk and its Relation to Fibre Diameter

By **D. K. Hill**

*Journ. Physiol.*, Vol. 111, 1950, pp. 283–303

It was known previously that the opacity of a crustacean nerve trunk undergoes a change when the nerve is stimulated. The present paper describes experiments for a further examination of the phenomenon. The effect is measured by making photoelectric recordings of the intensity of light scattered by the nerve. It was found that the opacity of the nerve is very sensitive to changes in fibre diameter, brought about by altering the osmotic pressure of the solution. When the fibres swell the opacity decreases, when they shrink it increases: a quantitative relation can be obtained.

Under some conditions there may be an initial, transitory, increase in opacity following stimulation; but the main effect is a decrease, and recovery takes 10–15 min. On the basis of known figures for ionic movements across a nerve membrane it is argued that this change in opacity is attributable to an increase in fibre diameter.

The dependence of opacity upon fibre size has been made use of in studying the permeability of the fibre membrane to certain solutes. D.K.H.

## The Volume Change Resulting from Stimulation of a Giant Nerve Fibre

By **D. K. Hill**

*Journ. Physiol.*, Vol. 111, 1950, pp. 304–27

There are reasons for supposing that stimulation of a nerve fibre causes an increase of the osmotic pressure in the interior. The fibre should therefore swell. The present paper describes a method for measuring the swelling of a cuttlefish nerve fibre following repetitive stimulation.

The relation between length and volume of a giant nerve fibre is also investigated; the volume is varied by altering the osmotic pressure of the external medium.

A study is made of the kinetics of water exchange across the fibre membrane resulting from a sudden change in the external osmotic pressure. D.K.H.

## The Males of *Canthocamptus bidens* Schmeil

By **Ashley G. Lowndes**

*Proc. Zool. Soc. London*, Vol. 120, 1950, pp. 395–403

There has been a considerable difference of opinion over the taxonomy of this species. In 1929 Chappuis created a new genus *Elaphoidella* and placed *Canthocamptus bidens* (Schmeil) in that genus. All taxonomists, so far as I am aware, followed Chappuis, with the single exception of Gurney, who not only disagreed with the creation of the new genus but also pointed out that there was no justification whatsoever for placing *C. bidens* in that genus, especially since the genus was founded almost entirely on the characteristics of the males. The recent discovery of the males and the structure of the fifth foot, among other things, have shown beyond question that Gurney was right so far as the taxonomy of *C. bidens* is concerned. A.G.L.

## The Autonomic Nervous System of the Chimaeroid Fish *Hydrolagus colliei*

By J. A. Colin Nicol

*Quart. Journ. Micr. Sci.*, Vol. 91, 1950, pp. 379–99.

The autonomic nervous system of the chimaeroid fish *Hydrolagus colliei* has been investigated by dissections and histological methods. It consists of a cranial parasympathetic portion and a sympathetic portion confined to the trunk. The latter extends from the level of the heart to the anus, and consists of segmentally arranged ganglia on each side of the dorsal aorta. These ganglia are closely associated with small accumulations of suprarenal tissue. Two axillary bodies are the largest of the sympathetic and suprarenal structures. They lie about the subclavian arteries and are made up of a gastric ganglion and a relatively large mass of chromaffin tissue. The sympathetic ganglia lie in an irregular plexus of longitudinal and crossing sympathetic strands but there is no regular sympathetic chain or commissure between ganglia. There are white rami communicantes which connect the sympathetic ganglia with spinal nerves. A small pregastric ganglion lies on the rami communicantes to the gastric ganglion. The visceral nerves arising from the sympathetic ganglia proceed to blood vessels, genital ducts, chromaffin tissue, and gut. The latter is supplied by large splanchnic nerves which originate in the gastric ganglia and proceed along the coeliac axis to the intestine, pancreas, and liver. Prevertebral ganglia are absent. A mucosal and a submucosal plexus are present in the intestine. The cranial component of the autonomic system comprises a midbrain and a hindbrain outflow. In the former there is a ciliary ganglion on the inferior oblique branch of the oculomotor nerve. Short ciliary nerves proceed from this branch to the eyeball. A radix longa is absent. Sensory fibres go directly to the eyeball from the profundus nerve as anterior and posterior long ciliary nerves. The hindbrain outflow comprises scattered nerve cells and ganglia on post-trematic branches of the glossopharyngeal and vagus nerves. These autonomic fibres in the branchial nerves innervate smooth muscle in the pharyngeal region. A visceral branch of the vagus innervates the heart, oesophagus, and intestine; it also establishes a connexion with the pregastric ganglion. In general, the autonomic nervous system of *Hydrolagus* is very similar to that of selachians. It appears that the autonomic systems of these two groups have undergone little alteration since their origin in the Palaeozoic from some common form. Their autonomic systems reflect a simple and primitive level of organization from which more complex systems of the bony fishes and amphibians have evolved. J.A.C.N.

# MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

## Report of the Council for 1950–51

The Council has to record with deep regret the deaths of the following former members of Council: Mr H. G. Maurice, C.B., who had represented the Ministry of Agriculture and Fisheries and the Zoological Society, and was a Vice-President; Prof. H. Gordon Jackson who had represented the British Association for the Advancement of Science; Dr R. S. Clark, a former member of the Scientific Staff of the Plymouth laboratory; and Sir Sidney F. Harmer, F.R.S., a member of Council since 1895, who had represented the Royal Society, and was a Vice-President; also Mr R. Hansford Worth and Mr Arthur W. W. Brown, Founders of the Association, the latter having been the last survivor of the original members.

### The Council and Officers

Four ordinary meetings of Council were held during the year, three in the rooms of the Royal Society, and one at the Plymouth laboratory. At these the average attendance was sixteen.

During the year the following new Governors have been appointed: Mr H. J. Johns, C.B., M.B.E., Fisheries Secretary, representing the Ministry of Agriculture and Fisheries in place of Mr P. D. H. Dunn, C.M.G., O.B.E.; Dr H. W. Parker, representing the Zoological Society; and Dr Edward Hindle, F.R.S., representing the British Association.

### The Plymouth Laboratory

The laboratory buildings have been kept in a good state of repair, and during the year all exterior wood and metal work has been painted. The dog-fish store house has been renovated; new fencing has been erected round the laboratory grounds. New wooden gates have been built at the entrance to the laboratory yard; these were made in the workshop from wood salved from the partitions between the cubicles in the original main laboratory.

During the year permission has been given by the Admiralty for the use of the facilities at Pier Cellars by certain members of the staff of the Plymouth laboratory; this small harbour in Cawsand Bay, with its storage accommodation, used to be rented by the Association before the war from the War Department.

### The Aquarium

The aquarium has continued to attract large numbers of adults and school children. All the tanks have been fully stocked and more pictorial labels, drawn by past and present students of the Plymouth City School of Art, have been added. There are now few exhibits in the large tanks without such labels.

Unusual animals to be seen in the tanks this year were Trigger-fish (*Balistes capriscus*), Boar-fish (*Capros aper*), Smelt (*Atherina presbyter*), and Sting-rays (*Trygon pastinaca*); a small Loggerhead Turtle (*Caretta caretta*) proved an attraction for several months.

### Research Ships

The research vessels *Sabella* and *Sula* and the motor-boat *Gammarus* have worked regularly throughout the year, except for brief periods necessary for general maintenance of hulls and machinery.

The Association is indebted for the loan from the Admiralty of an improved type of transportable outboard echo-sounder to replace that at present fitted in the *Sabella*.

### The Staff

Mr G. A. Steven has been promoted to the grade of Senior Principal Scientific Officer as from 1 April 1950. Mr J. Lowy was appointed to the staff of the Plymouth laboratory in October 1950, in the grade of Scientific Officer.

Dr D. P. Wilson attended a meeting of the Centre National de la Recherche Scientifique in Paris in February 1950, where he was invited to read a paper on 'Larval Metamorphosis and the Substratum'.

Dr W. R. G. Atkins, F.R.S., and Dr Mary Parke attended the meeting of the Seventh International Congress of Botany at Stockholm in July 1950, at which Dr Atkins was invited to read a paper.

Mr G. A. Steven attended the thirty-eighth meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1950.

Mr H. W. Chang, of the Academia Sinica, Shanghai, was appointed Ray Lankester Investigator to work at the Plymouth laboratory during 1950.

### Occupation of Tables

The following one hundred and five workers have occupied tables at the Plymouth laboratory during the year:

E. ADAMS, Plymouth (Library).
Miss E. B. ALBRECHT, London (Behaviour of *Arenicola*).
Mrs F. R. ALLISON, Oxford (Cocoon formation in Platyhelminths).
Miss G. AUDY, London (Islets of Langerhans in *Lophius*).
Rev. B. AUSTIN, Southsea (Marine bacteriology).
R. BAINBRIDGE, Oxford (Plankton interrelationships).
Miss D. BALLANTINE, Development Commission (Taxonomy and culture of marine Flagellates).
Dr D. BARKER, Oxford (General).
Prof. E. J. W. BARRINGTON, Nottingham (Cytology of Elasmobranch pancreas).
Dr ELIZABETH J. BATHAM, Cambridge (Nerve net of sea anemones).
L. G. E. BELL, London (Library).

A. C. G. Best, London (Histology of marine animals).
Prof. M. L. Bhatia, Delhi (Morphology of *Pontobdella muricata*).
Dr Anna M. Bidder, Cambridge (Library; digestive mechanism in Cephalopods).
M. Blackburn, Australia (General).
Dr H. Blaschko, Oxford (Amine oxidase in *Octopus* liver).
Dr B. P. Boden, Cape Town (Phytoplankton and Euphausians).
B. B. Boycott, London (Brain of *Octopus* and *Sepia*).
Prof. T. Braarud, Oslo (Phytoplankton).
L. R. Brightwell, East Horsley (General).
Miss E. M. Brown, London (Parasitic Dinoflagellates).
Dr P. Buffa, Oxford (Effects of sodium fluoracetate on marine animals).
Dr M. Buljan, Split, Yugoslavia (Chemical oceanography).
Dr T. H. Bullock, Los Angeles (Comparative neurophysiology).
A. Bursa, Kenton (Dinoflagellates; *Prorocentrum*).
G. W. Cambridge, London (Comparative physiology).
H. W. Chang, Academia Sinica, Shanghai (British Council Scholar and Ray Lankester Investigator) (Biology of *Callionymus*).
Dr P. N. J. Chipperfield, Brixham (Library).
Miss E. Clay, Brixham (Phytoplankton culture methods).
Dr K. W. Cleland, London (*Echinus* eggs).
Miss M. Collis, London (*Sabellaria*).
J. S. Colman, Port Erin (General).
R. H. Cook, Cambridge (General).
F. R. Coombe, Plymouth (Physical properties of sand grains).
B. G. Cragg, Cardiff (Neurophysiology of *Sepia* and *Loligo*).
Miss G. Creek, London (Lamellibranchs).
Dr D. J. Crisp, Brixham (Library).
Dr Doris R. Crofts, London (Muscle morphogenesis of Archaeogastropods).
R. I. Currie, National Institute of Oceanography (Physical Oceanography).
Dr R. Phillips Dales, London (Ecology of *Nereis diversicolor*).
J. H. Elgood, Nigeria (Library).
D. Etherington, London (Coccidian parasites).
Dr P. Fatt, London (Nerve muscle system in Crustaceans).
Dr Maria Felinska, Cheltenham (Ciliates).
G. R. Forster, D.S.I.R. (Biology of prawns).
H. C. Fountain, Torpoint (Marine Acarines).
Dr Vera Fretter, London (*Turbonilla elegantissima*).
Dr Helen Goodrich, Oxford (Parasites in *Leander* and Polychaetes).
Dr Isabella Gordon, British Museum (Nat. Hist.) (Decapod Crustaceans).
C. O. Granger, Ministry of Supply, Windscale (Chemical Oceanography).
Dr J. J. Groen, Utrecht (Physiology of Elasmobranch labyrinth).
Dr J. P. Harding, British Museum (Nat. Hist.) (Chromosomes in *Calanus*).
Dr T. J. Hart, National Institute of Oceanography (Plankton).
Miss J. Hawkins, Oxford (Amine oxidase in *Octopus* liver).
M. N. Hill, Cambridge (Geology of the English Channel).
G. A. Horridge, Cambridge (Nervous system of Polychaetes).
G. Hoyle, London (*Phallusia*).
O. D. Hunt, Newton Ferrers (Fouling organisms).
F. R. Johnson, Accra, Gold Coast (General).
Dr F. R. Harden Jones, Cambridge (Swim bladder of fishes).
W. C. Jones, Cambridge (Spicule formation in *Leucosolenia*).

K. A. Joysey, London (Geographical distribution of *Echinoderms*).
Dr Elizabeth M. Kampa, Cape Town (Retinal pigment in fish).
Dr B. Katz, London (Nerve muscle system in Crustaceans).
R. S. Keir, Development Commission (Development of Lamellibranchs).
Dr G. Y. Kennedy, Sheffield (Porphyrins in marine animals).
Prof. W. B. R. King, F.R.S., Cambridge (Geology of the English Channel).
Dr F. G. W. Knowles, Marlborough (Library).
Miss P. Kott, Australia (Biology of Tunicates).
Dr Marie V. Lebour, Cawsand (Decapod Crustaceans).
Miss H. M. Lloyd, London (Reproductive systems of Tectibranchs and Nudibranchs).
Dr O. Lowenstein, Glasgow (Physiology of Elasmobranch labyrinth).
Dr A. G. Lowndes, Wells (Entomostraca).
J. Lowy, Cambridge (Muscular contraction in Lamellibranchs).
M. F. Mahmoud, Manchester (*Scalpellum* and *Balanus*).
A. W. Mansfield, Cambridge (General).
Dr Sidnie M. Manton, F.R.S., London (Locomotion of Arthropods).
N. A. Mitchison, Oxford (Regeneration in *Sycon* and *Grantia*).
Miss M. Morris, Oxford (Luminescent Copepods).
J. E. Morton, London (Marine Pulmonates).
Inst.-Lieut. H. C. Parmenter, R.N., Admiralty, London, (Physical Oceanography).
Miss G. D. Parry, Glasgow (Sea anemones).
Prof. R. A. Peters, F.R.S., Oxford (Effect of sodium fluoracetate on marine animals).
Dr L. E. R. Picken, Cambridge (Comparative study of chitins).
Dr W. J. Rees, British Museum (Nat. Hist.) (Larvae of Cephalopods).
G. A. Robinson, Development Commission (Phytoplankton).
D. J. Rochford, Australia (General).
Miss H. G. Q. Rowett, Plymouth (Library).
P. Sevenster, Oxford (Breeding and behaviour of *Spinachia*).
Prof. J. E. Smith, London (Nervous system of Polychaetes).
S. E. Smith, Oxford (Regeneration in *Sycon* and *Grantia*).
A. J. Southward, Port Erin (General rock fauna).
C. P. Spencer, Bangor (Physiology of Diatoms).
Miss F. A. Stanbury, Plymouth (Library).
Miss M. F. Sutton, London (Regeneration in *Ciona*).
Dr N. Tinbergen, Oxford (Breeding and behaviour of *Spinachia*).
E. R. Trueman, Hull (Elasticity of bivalve ligaments).
D. Vaux, Lowestoft (Physical oceanography).
Dr A. J. H. Vendrik, Utrecht (Physiology of Elasmobranch labyrinth).
Dr P. Vonwiller, Zurich (Nervous system of prawns).
P. R. Walne, Conway (Chemistry of sea water).
G. P. Wells, London (*Arenicola*, *Chaetopterus* and *Sabella*).
Dr Kr. Fr. Wiborg, Bergen (Fisheries and plankton).
W. Wieser, Vienna (Ecology of free-living Nematodes).
Dr J. D. H. Wiseman, British Museum, (Nat. Hist.) (Geology of the English Channel).

As in recent years, since the war, there has been a regular flow of scientists making visits of a day or so to see the work of the laboratory, or discuss problems with the staff. The following visitors have come from overseas: Dr C. O'D. Iselin, Woods Hole; Dr P. Ullyott, Istanbul; Prof. Bernhard Peyer, Zurich; A. E. Greenberg, U.S.A.; Dr V. Tonolli, Pallanza; Dr W. F.

Clapp, Duxbury, Mass.; Dr Herbert Graham, Miami; Mr and Mrs A. R. A. Taylor, Prince Edward Island; Dr H. A. L. Trampusch, Amsterdam; Prof. H. Grundfest, Columbia University; Prof. Gilbert M. Smith, Stanford University; B. Komarofsky, Haifa; B. S. Kisch, St Jean de Luz; Dr C. G. Schmitterlöw, Stockholm; Dr L. A. Walford, Washington, D.C.; Dr V. D. Vladykov, Quebec; Dr E. Wubben, Leiden; Lt.Cdr. W. J. Perry, U.S.N.; and Capt. S. Mahagita, Thailand.

A number of research ships have visited Plymouth during the year and afforded opportunities for members of staffs to meet and take part in useful discussions. These have been R.R.S. *Discovery II*, F.R.V. *Sir Lancelot*, H.M.S. *Challenger*, R.R.S. *William Scoresby*, and H.M. Danish Ship *Galathea*, which left in October for a two-year research voyage under the scientific leadership of Dr Anton Fr. Bruun.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by forty-four students from the following Universities and University Colleges: Oxford, Cambridge, Glasgow, Edinburgh, London, Liverpool, Leeds, Sheffield, Reading, Southampton, Cardiff, Bangor, Newcastle, Hull and Leicester, and from Medway Technical College.

Also during the Easter Vacation, Mr R. J. Jones brought a party of seven boys from Whitgift School and Mrs F. B. J. Sewell a party of two teachers and nine pupils from Southampton Girls' School.

An Advanced Course in Experimental Zoology, conducted by Dr J. A. C. Nicol, was held during the Summer Vacation and was attended by fourteen students.

A meeting of the Society for Experimental Biology was held at the Plymouth laboratory from 27 to 29 September 1950. Some ninety members attended the meeting, at which there were a number of contributions from members of the laboratory staff.

## Scientific Work of the Plymouth Laboratory Staff

### *Physics and Chemistry of Sea Water*

Measurements of daylight have been continued by Dr W. R. G. Atkins, assisted by Miss P. G. Jenkins, and the results for 1947, 1948 and 1949 are nearly ready for publication. These can now be compared with similar measurements made during 1947 and 1948 by Dr J. M. Stagg at Kew, using a selenium instead of a sodium cell.

Work on the scattering of light in water has been continued by Dr H. H. Poole, Dr Atkins and Mr F. J. Warren, and the seasonal changes in sea water have been studied. Scattering is greatest at the surface and shows no marked change at a thermocline. Forward and back scatter are closely the same in distilled water, but in tap water and in sea water forward scatter may be from three to ten times the greater, according to the angle and quantity of suspended matter. For distilled water the scattering in the minimum position, a little less than 90° with respect to the beam, is about one in two or three million of the total flux, so every possible precaution has to be taken to avoid the smallest trace of light from unwanted sources.

During trials following recommissioning the two vessels of the National Institute of Oceanography collected water and plankton samples from over the continental slope of the Celtic Sea for Dr L. H. N. Cooper. The first determinations of total phosphorus in the deep water of the Atlantic slope collected by R.R.S. *Discovery II* gave around 1·3 mg.-atom/m.$^3$P between 800 and 2000 m. depth rising to 1·6 mg.-atom/m.$^3$ at 3800 m. Between 2000 m. and the bottom at 4000 m., in water that otherwise has markedly uniform properties, the silicate content was found to be doubled—from 20 to 41 mg.-atom/m.$^3$ Si.

In the upper waters south-west of Ireland examined by R.R.S. *William Scoresby* in January the content of total and inorganic phosphorus was lower than had been expected. Partly to follow this information up and partly to supplement the investigations of the Lowestoft research vessel *Sir Lancelot* in the English Channel, cruises were made in the Celtic Sea by R.V. *Sabella* in April and June, and by R.R.S. *Discovery II* in May. Much of the Celtic Sea proved to be relatively poor in total phosphorus ($<$ 0·6 mg.-atom/m.$^3$). In the neighbourhood of the Labadie Bank regeneration of inorganic phosphate seems to be occurring from the muddy bottom deposits which occur there.

Water relatively rich in nutrients was found off the Pembrokeshire shore of the Bristol Channel. This enrichment is probably due to the sewage of urban South Wales and to the run off from the fertile watershed of the Severn, Usk and Wye. The Smalls fishing ground comes within the area of enrichment.

Information on the nature of the currents which run round Ushant, Land's End and St David's Head was obtained. Observations crucial for the completion of the papers on themes put forward in previous Reports have been made.

Close and fruitful co-operation has been maintained with Dr J. N. Carruthers and his colleagues at the Hydrographic Department of the Admiralty, and with the Ministry of Agriculture and Fisheries Laboratory at Lowestoft who have this year carried out extensive hydrographical and biological investigations in the English Channel.

In all this work the method for the analysis of total phosphorus in sea water developed by Dr H. W. Harvey has proved of much value. With it one may not only assess potential productivity but also the movements of water masses.

Mr F. A. J. Armstrong has continued the monthly cruises to Station E1 and has made the routine determinations of inorganic phosphate and total phosphorus. In addition, since May 1950, silicate has been determined by a sensitive molybdenum-blue method, of which an account is being prepared for publication. Mr Armstrong has also undertaken all the analyses of inorganic phosphate, total phosphorus and silicate on the samples collected from the

Celtic Sea by R.V. *Sabella*, R.R.S. *William Scoresby* and R.R.S. *Discovery II*, and a number for total phosphorus collected in the English Channel by F.R.V. *Sir Lancelot*.

He has confirmed that long storage of sea water in glass bottles causes leaching of iron from the glass. Some bottles used for the total phosphorus estimation have been found to release phosphate into the water kept in them. These effects have been overcome by the use of small polyethylene bottles, of which the laboratory has acquired some 300.

Dr H. W. Harvey has collaborated in several investigations bearing upon the production of plant life in the sea. With Dr R. A. Cox, of the National Institute of Oceanography, a photoelectric instrument was built which allows accurate colorimetric estimations to be made on board ship. This was required, and has been in use in R.R.S. *Discovery II*, for estimating phosphate, nitrate, nitrite, silicate and iron in the sea. With Dr M. Buljan of the Institute for Oceanography and Fisheries, Split, Yugoslavia, the several methods of estimating ammonia in sea water have been examined; a development of the principle used by Teorell promises to allow reasonably rapid and precise estimations of ammonia in sea water without distillation.

Many experimental observations have been made concerning the effect of added substances other than available nitrogen, phosphorus, iron and manganese on the growth rate of diatoms, and concerning their different growth rates when sown in waters collected from different positions in the sea. For an interpretation of these observations it has become necessary to evolve techniques to control conditions, such as the presence of associated bacteria and the intensity and periodicity of illumination. Control of these conditions is also necessary to confirm observations of direct utilization of organic phosphorus compounds by these plants; to ascertain the range of organic nitrogen compounds which can be utilized directly without prior breakdown by bacteria; and to investigate the adaptation which takes place when a diatom is transferred from a nitrate to an ammonium source of nitrogen supply and vice versa. In connexion with this, Dr C. P. Spencer, of the Bangor Marine Laboratory, has made observations on the growth of diatoms and, by growing the diatoms for several seven-day periods in culture media containing both streptomycin and penicillin, has obtained cultures from which no bacterial growth can be induced in a variety of media. He has also started observations on the kinetics of diatom growth of a similar type to those which have already thrown light upon various bacterial metabolic processes.

Estimations of the chlorophyll content of surface water at E1 have been made by Dr Atkins during 1948 and 1949. The maximum weight of chlorophyll found was 4·3 mg./m.$^3$, comparable with Krey's figure of 5 mg. for Kiel, and Riley's 3·6 mg. for the North Atlantic. In collaboration with Dr Parke he used pure algal cultures to determine the number of cells required to give 1 mg. of chlorophyll. Trouble due to yellowish tints was eliminated by using red colour filters. Of nine cultures six were between 50 and 750 million cells per milligram. These results, which were published in Vol. 29, No. 3, of the *Journal*, show that only the very smallest and therefore most numerous species would provide one cell in each haemocytometer field (0·1 mm.$^3$) of natural sea water, if all the chlorophyll found at the maximum, 4·3 mg./m.$^3$, were contributed by that one species.

### *Plankton*

Dr Mary Parke has continued the study of the small flagellate and non-motile forms in the sea water off Plymouth. About seventy different organisms, not including diatoms, have now been isolated and are being maintained in species-pure culture for further study. The contamination of some of the cultures by fungal growth brought in by tiny flies during the summer has caused considerable trouble, and a great deal of time has been and is being spent in clearing the cultures of the fungus.

This year organisms present in samples of sea water which were taken at least 70 miles offshore have been cultured and examined. These samples were kindly collected by Dr L. H. N. Cooper, and by Dr D. H. Cushing of Lowestoft. The few samples that have been examined show that the same flagellate forms occur frequently in both inshore and offshore waters. A number of these organisms have been obtained from the Tamar Estuary, Knap Buoy, Stations L4 and E1, and the offshore stations worked by Dr Cooper and Dr Cushing. The forms recognized so far are *Pyramimonas grossii*, *Stichococcus* n.sp., *Prorocentrum micans*, *Massartia rotundata*, *Hemiselmis rufescens*, a 1–2 $\mu$ yellow green flagellate containing chlorophyll, *Dicrateria gilva*, *Pseudopedinella* n.sp., and three other undescribed chrysomonads, two of which possess three flagella.

At least six different species of flagellates possessing three flagella have been isolated from sea water off Plymouth. These flagellates belong to the Chrysophyceae but cannot be placed in the only described genus with three flagella, *Prymnesium*. Experiments, set up by Mr S. M. Nunn, are now in progress to see if these flagellates, like *Prymnesium parvum* Carter, produce a specific poison which is fatal to fish.

Mr G. A. Robinson, on a Development Commission Fisheries Research Training Grant, has been studying the production and vertical distribution of phytoplankton in the Plymouth area throughout the year 1950. The spring outbreak was late and prolonged, and lasted until the end of April when the numbers fell very low. There was an outburst of *Skeletonema costatum* in June and of *Rhizosolenia alata* Brightwell var. *genuina* Gran. in July. The autumnal outburst occurred at the end of August, carrying on until the beginning of October.

Results of samples taken at various depths showed that in a depth of approximately 50 m. the diatoms were evenly distributed throughout the water column when vertical mixing occurred in winter and spring. In the summer, when the thermocline was established, there was some evidence to show that there may have been two communities of diatoms, above and below the thermocline.

Mr Robinson has assisted Dr Parke in the maintenance of the stock cultures of marine flagellates and diatoms, paying special attention to the latter. Subcultures have been sent to a large number of institutions in this country and abroad for research purposes.

The weekly half-hour oblique hauls with the 2 m. stramin ring-trawl have been continued during the year. Preliminary inspection of the catches by Mr P. G. Corbin shows a possible slight improvement in macroplankton production over the low level of the last few years; there has not, however, been a pronounced increase. A note by Mr Corbin on pilchard spawning in the central English Channel in 1947 and 1948 was published in Vol. 29, No. 1, of the *Journal*. The material was taken in plankton collections made by members of the scientific staff of the British Museum (Natural History) during cruises of Major H. W. Hall's M.Y. *Manihine*, and was very kindly placed at the disposal of the Marine Biological Association by the Director and Trustees of the Museum.

During the last two years Dr D. P. Wilson has examined the possibility of the existence of a difference in biological properties between waters from the English Channel off Plymouth and from the Celtic Sea west of the Isles of Scilly. He has succeeded in showing that such a difference exists. Experiments made mainly with eggs and larvae of the sea urchin, *Echinus esculentus*, but also with those of the worms, *Ophelia bicornis* and *Sabellaria alveolata*, have shown that they often develop abnormally, or are in poor condition, in filtered sea water from the region of the Eddystone, but that they are usually normal and healthy in filtered water from the Celtic Sea. They also develop normally and healthily in a mixture of equal proportions of both kinds of water. The indications are that the Eddystone water lacks some constituent essential for healthy development, which is present in Celtic Sea water. The result accords with the hydrographical and biological changes which have taken place in the area within recent years. A paper on this work has been prepared for the *Journal*. In this research Dr Cooper has been of great assistance in collecting and interpreting the hydrographic data.

### *Fauna and Flora of the Sea Floor*

Dr D. P. Wilson has spent some time, partly with the assistance of Mr F. R. Coombe of Devonport High School for Boys, investigating the physical properties of sands from the Exmouth district, with the aim of finding some clue to the means whereby the larvae of the polychaete worm, *Ophelia bicornis*, distinguish the sand of their adult habitat from similar sands in which the species does not live. The data obtained are fairly extensive but it is as yet uncertain how far they will prove applicable to the problem. During the breeding season further experiments on the settlement reactions of the living larvae gave substantial support to the idea that certain sands repel the larvae by virtue of some substance strongly adhering to the grains and that this substance can be removed only by drastic treatments. There is some evidence, not yet conclusive, that this substance can be transferred to 'clean' grains by physical contact. There is, at present, little indication of its nature. The ability of the larvae to distinguish between sands inhabited and uninhabited by the adults was strikingly demonstrated in a number of experiments in which they were given the opportunity to choose between them. The results of many experiments are only now being critically examined.

Mr N. A. Holme has been making a survey of the bottom fauna in the immediate neighbourhood of Plymouth, using the new 'scoop' sampler. Samples are being taken at twenty stations both inside and outside the Eddystone, an area of $\frac{1}{2}$ m.$^2$ being sampled at each station. The survey will provide data on the biomass of the macrofauna to provide a basis for following long-term changes in the productivity of the area. At the same time, information is accumulating on the distribution of certain lamellibranch molluscs in relation to the grade of soil. This is being supplemented where possible by observations on the same species living on the shore.

Further attempts are being made by Mr Holme to devise more efficient and more easily handled bottom-sampling gear.

He has now completed a paper on the systematics of the genus *Ensis*. Shell characters alone have been found insufficient for certain identification, and a reliable character has been found in the form and arrangement of the papillae surrounding the fourth pallial aperture. The results were published in Vol. XXIX, No. 3, of the *Journal*.

Over the past two years the small-scale distribution of *Tellina tenuis* on a sandbank in the Exe estuary has been studied. The distribution of individuals was found to be non-random, tending towards an even distribution. It is possible that each shell delineates a 'territory' on the soil surface as a result of the activities of its long inhalent siphon, and this may be the cause of the observed distribution. The results of this work have been published in Vol. 29, No. 2, of the *Journal*. It is hoped to continue this line of study through observations in tanks in the laboratory, but attempts to keep *Tellina* in a healthy condition under artificial conditions have not yet been successful.

Dr H. G. Vevers has continued his work on underwater photography as a means of estimating the density of epifaunal invertebrates. The main technical problem has been the provision of an adequate light source. This has now been solved by fitting to the apparatus an increased number of large photoflood lamps. With this array many photographs have been taken on the trawling grounds off Plymouth and Looe. An interesting series of pictures taken in an area near Looe Island shows a very rich population of *Ophiothrix* *fragilis*; these are not distributed evenly on the sea-bed, but are massed in groups, with the individual brittle-stars often lying one above the other. A paper describing the apparatus and some preliminary results is in preparation. In addition, a paper has been published in Vol. 29, No. 3, of the *Journal*, giving observations on the parasitization of *Asterias rubens* gonads by the ciliate *Orchitophrya stellarum*, and also a note confirming the presence in the Plymouth area of the rare ophiuroid *Ophiopsila annulosa* (*Journal*, Vol. 29, No. 1).

In an attempt to analyse the very varied coloration found in natural populations of *Asterias rubens*, Dr Vevers has done some preliminary work on carotenoid pigments of starfish, and in collaboration with Dr G. Y. Kennedy, of the Department of Cancer Research, University of Sheffield, on the porphyrin pigments in the starfish integument.

Mr G. M. Spooner has continued to study the amphipod crustaceans with a view to acquiring more complete knowledge of the fauna of south-west Britain, and to deal with outstanding taxonomic problems. A paper has been prepared for publication giving further information on *Gammarus zaddachi oceanicus*. From an examination of fresh British material its status in Britain could be described for the first time. It occurs in the north—on the west coast of Scotland southward to the Clyde area, and on the east coast to north-east Yorkshire. This matches its occurrence on the Continent (southward to Heligoland, east Denmark and Baltic Sea). In sheltered west Scottish habitats it may be plentiful amongst brown algae in the lower half of the tidal zone. Additional information on its world range is also presented, partly from re-identifications of records in the literature where biometric data or illustrations render this possible. The form has a wide range in subarctic regions, occurring from the Siberian coasts, at least from 140° E., westward to Greenland and north-eastern America. Until recently it had passed under the all-embracing name of *G. locusta*, which strictly should refer to a species which is abundant on the shore of temperate and southern Europe, but does not spread into the arctic-boreal regions. Nor does *G. locusta* seem to occur in America, and it is emphasized that the common species which normally goes under that name on the Atlantic seaboard of Canada and the U.S.A. is really *G. zaddachi oceanicus*.

An investigation by Mr Spooner of the composition of populations of *Jassa falcata* is throwing new light on the old problem of its so-called polymorphism.

Mr G. R. Forster, on a D.S.I.R. maintenance grant, has studied the biology of *Leander serratus*, the common prawn. Samples have been taken throughout one year to provide data on the rate of growth and the breeding season. The youngest prawns appeared inshore during July in pools at or above mid-tide level. By October their mean length was approximately 5·25 cm. in 1950 and 6·25 cm. in 1949. This difference may possibly be related to the fact that in 1949 the sea temperature remained above 15° C. six weeks later than in 1950. Subsequently, the females showed a slightly higher growth rate than the males. It is unlikely that more than occasional prawns survive their third summer. A paper is now being prepared on the age and growth, breeding, and food of this species.

Collections of ascidians, especially the compound forms, have been made by Miss P. Kott of C.S.I.R.O. Fisheries Division, Australia, who has been working at the Plymouth laboratory during the past year. Species not already represented have been added to the laboratory museum, and a new species, *Corella halli*, has been described showing an interesting intermediate condition of the branchial sac. This specimen was obtained by Major H. W. Hall's yacht *Manihine* when collecting for the British Museum (Natural History) in the English Channel.

Dr Parke has devoted much time to the revising of the late Mr G. F. Tregelles's manuscript on the marine algae of Devon for part II of the 'Flora of Devon', published by the Devonshire Association. This manuscript was prepared in 1939, and a great deal of work is needed to bring the nomenclature up to date and to add the recent records.

### *Physiology of Marine Organisms*

Dr J. S. Alexandrowicz has continued his study of the special muscle units in crustaceans which, together with their associated nerve cells, may be regarded as muscle receptor organs. By means of methylene-blue staining it has been found that these organs are represented on each side of the abdominal segments by two units, and from the different structure of the muscle elements of each unit of a pair it may be concluded that they are not physiologically identical. In the nerves supplying the muscle receptor organs three kinds of fibres could be distinguished, most probably having different functions.

In the embryonic lobster stained with methylene blue it has been possible to identify the nerve cells of these muscle receptors and to establish that the axons of these cells, after reaching the ganglionic cord, form a tract running through all the abdominal and thoracic segments. It was found that the nerve cells of the muscle receptor organs are identical with elements described as sensory cells by E. J. Allen in his work on the nervous system of the lobster embryo. A paper on the results of this research has been accepted for publication in the *Quarterly Journal of Microscopical Science*.

In October and November 1950, Dr Alexandrowicz spent his leave working at the Stazione Zoologica, Naples, where he continued researches made before the war on the nervous system of stomatopods.

Further work on the nervous system of the sabellid, *Branchiomma vesiculosum*, by Dr J. A. C. Nicol, has revealed that this worm has a giant axon arrangement very similar to that of *Myxicola*, which has already been described. Electrical stimulation of the axons gives rise to single muscle twitches, one per stimulus, with no evidence for facilitation. These results are being published in the *Journal of Experimental Biology*. The action of drugs on the neuro-muscular junction has also been investigated. This study has revealed an essentially cholinergic system, with acetylcholine and nicotine giving the greatest effects.

Additional observations on photosensitivity in *Branchiomma*, continued by Dr Nicol from last year, have shown that these animals can give all their usual light responses without their eyes. Some preliminary observations to the contrary, reported earlier, are ascribed to sensory fatigue.

Mr J. Lowy, who joined the staff in October, has continued work started at Cambridge concerning the mechanism of contraction in the muscles of *Mytilus edulis*. In an attempt to discover whether both tonic and phasic contractions in these muscles are accompanied by expenditure of energy, experiments are now in progress in which simultaneous records are made of the electrical and mechanical activity in the adductor muscles of intact animals.

Miss P. Kott has been attempting to measure the rates of oxygen consumption of the ascidian, *Ascidiella aspersa*; difficulties have been encountered in removing the plant material from the test and results are as yet inconclusive. Results obtained from Winkler titrations using the whole animal are being supplemented by results obtained from tissue slices in Warburg manometers. There are indications that the strength of illumination may inversely affect the amount of oxygen used by the animal. Later the effects of various respiratory inhibitors on different species are to be tested.

Kymograph drum recordings of movements in the species *Ciona intestinalis*, *Ascidia aspersa* and *Molgula manhattensis* have been made; there are rhythms in contraction of both the atrial and branchial siphons, but these are extremely variable and as yet no specific distinctions have been made, either in type of movement, magnitude or frequency; it is hoped to continue this work.

Mr Spooner has maintained contact during the year with the Radiobiological Research Unit and the Chemistry Department of A.E.R.E. Harwell, whom he has supplied with annotated abstracts of the literature dealing with the concentration of certain minor constituents of sea water.

### *Fish and Fisheries*

Mr G. A. Steven has continued his work on the biology of the mackerel. Owing to the very long spawning period of these fish (March–September inclusive) and their extremely rapid growth during early life it has proved difficult to extract precise results from the mass of data collected. Most difficulties have now been largely overcome and more definite assessments of age and growth have been made. These agree very closely with the provisional results given in last year's report. It now also appears that about half a full year's growth takes place during the four months May to August inclusive.

The gonads of nearly ten thousand fish have been examined, the sex determined and maturity stages recorded. From these and other data it appears that many fish reach maturity during their second year of life at lengths of about 28 cm. and upwards. There is, however, great variability, spent fish of smaller size being not uncommon while others are still in virgin condition at lengths of 32 cm. or more. There is also some evidence to suggest that in relatively small fish of not more than 28 cm. the gonads often progress a considerable way towards ripeness and then assume a spent appearance without any actual spawning having taken place. A paper embodying the results of this work is nearing completion.

Further study by Mr P. G. Corbin of the sand-eels of the Plymouth area has resulted in the identification of a new species, *Ammodytes immaculatus* (*Nature*, Vol. 166, p. 525). This is evidently the adult of a post-larva which when first described in Vol. 28, No. 1, of the *Journal* could not be attributed to a known adult. An adult specimen of *A. marinus* Raitt was taken in Start Bay in May 1950. The post-larva of this species occurs in the Plymouth area but not in such large numbers as in Scottish waters, the southern North Sea and the eastern Channel. Several years' collections of *Ammodytes* post-larvae from those areas have now been examined by Mr Corbin through the courtesy of the Directors of the Fisheries Laboratories of Aberdeen and Lowestoft. The occurrence of only one adult *A. marinus* in the Plymouth area during twelve months' employment of a trawl with a fine-mesh cover on the cod-end, together with the comparative scarcity of the post-larvae, tend to confirm the suggestion that the range of the species does not extend southwards of a line joining south-west Ireland, Land's End and the Channel Islands.

Mr H. W. Chang, British Council Scholar and Ray Lankester Investigator, has continued to work on the biology of *Callionymus* in the Plymouth area. The rate of growth of the male *C. lyra* falls into three main categories. In those males which breed in the third year the growth rate in the first year is normally higher than that of the second year; but in those which breed in the fourth year it is usually highest in the second year. The growth rate of those males breeding in the fifth year is highest either in the second or in the third year. These differences are probably related to sexual maturity rather than racial characters. Similar differences in growth rate also occur in the female, but it is difficult to find the proper standard by which to treat them separately.

After obtaining detailed information on the type specimens from the Museum National d'Histoire Naturelle, Paris, and examining Mediterranean specimens, it is evident that the third species of *Callionymus* found off Plymouth is not *C. fasciatus* as was originally thought. It is *C. reticulatus* C. & V., which hitherto has not been recorded from British waters and has now been shown to occur also in the southern North Sea as well as off the coast of Portugal.

Mr P. G. Corbin, in co-operation with Mr Steven, has developed a bridle suspension for a conical tow-net which eliminates the necessity for a metal ring at its mouth. When fishing, the net maintains a rigidly circular opening, and it is towed from a single warp. The principle is applicable to tow-nets of the usual sizes, and successful trials have been made with a net of 9 ft.

(*c*. 2¾ m.) diameter at the mouth, towed at speeds from 1 to 4½ knots: it seems probable that this net could be fished at greater speeds. It is hoped at the next stage to work a net of this design having a diameter of some 30 ft. Experiments on the development of a depressor for use with this net are also being made.

Now that access to the Pier Cellars basin is again available some further experiments on rope and net preservation have been started. Contrary to expectation, it has been found that the supposed waterproofing of ropes, claimed for a commercial treatment, leads to little or no diminution in the uptake of water when equilibrium has been attained. Rather more water was in some cases taken up, especially with waterproofed sisal. All ropes sank immediately except untreated coir. The sum of the residual preservative, after evaporation of solvent, and of water uptake was found to be approximately constant.

## Library

The thanks of the Association are again due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association.

Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated. We are grateful to Mrs E. W. Sexton for the gift of thirty volumes of the *Transactions of the Devonshire Association*; to Dr A. G. Lowndes for the gift of Rideal's *Introduction to Surface Chemistry*, Alexander and Johnson's *Colloid Science* (2 volumes) and Kanthack and Goldsmith's *Table of Refractive Indices* (2 volumes), as well as for many reprints; and to Messrs Macmillan and Co. for six books, all of which are valuable additions to the Library.

The Library has lately been much used by visiting members of the Association.

## Published Memoirs

Volume 29, No. 1, of the *Journal* was published in April 1950, No. 2 in September 1950, and No. 3 in February 1951.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ALEEM, A. A., 1950. The occurrence of *Eurychasma Dicksonii* (Wright) Magnus in England and Sweden. *Medd. fr. Göteborgs Bot. Trädgärd*, XVIII, pp. 239–45. (*Contr. Mar. Bot. Inst. Göteborg*, No. 2.)

BATHAM, E. J. & PANTIN, C. F. A., 1950. Muscular and hydrostatic action in the sea-anemone *Metridium senile* (L.). *Journ. Exp. Biol.*, Vol. 27, pp. 264–89.

BATHAM, E. J. & PANTIN, C. F. A., 1950. Inherent activity in the sea-anemone, *Metridium senile* (L.). *Journ. Exp. Biol.*, Vol. 27, pp. 290–301.

Batham, E. J. & Pantin, C. F. A., 1950. Phases of activity in the sea-anemone, *Metridium senile* (L.), and their relation to external stimuli. *Journ. Exp. Biol.*, Vol. 27, pp. 377–99.

Bidder, Anna M., 1950. The digestive mechanism of the European squids, *Loligo vulgaris*, *Loligo forbesii*, *Alloteuthis media* and *Alloteuthis subulata*. *Quart. Journ. Micr. Sci.*, Vol. 91, pp. 1–43.

Cooper, L. H. N., 1950. The nitrogen cycle. *Chambers's Encyclopædia:* 1950.

Corbin, P. G., 1950. *Ammodytes immaculatus*, a new species of sand-eel found in European seas. *Nature*, Vol. 166, pp. 525–6.

Dresel, Elisabeth I. B. & Moyle, Vivien, 1950. Nitrogenous excretion of Amphipods and Isopods. *Journ. Exp. Biol.*, Vol. 27, pp. 210–24.

Hanson, Jean., 1950. The blood-system in the Serpulimorpha (*Annelida*, *Polychaeta*). II. The anatomy of the blood-system in the Sabellidae, and comparison of Sabellidae and Serpulidae. *Quart. Journ. Micr. Sci.*, Vol. 91, pp. 369–78.

Haywood, C. A. & Moon, H. P., 1950. The mechanics of the blood vascular system of *Ascidiella aspersa*. *Journ. Exp. Biol.*, Vol. 27, pp. 14–28.

Hill, D. K., 1950. The effect of stimulation on the opacity of a crustacean nerve trunk and its relation to fibre diameter. *Journ. Physiol.*, Vol. 111, pp. 283–303.

Hill, D. K., 1950. The volume change resulting from stimulation of a giant nerve fibre. *Journ. Physiol.*, Vol. 111, pp. 304–27.

Holme, N. A., 1951. Sampling the sea-bed. *Discovery*, February 1951, pp. 59–63.

Hörstadius, Sven, Lorch, I. J. & Danielli, J. F., 1950. Differentiation of the sea urchin egg following reduction of the interior cytoplasm in relation to the cortex. *Exper. Cell Res.*, Vol. 1, pp. 188–93.

Keynes, R. D. & Lewis, P. R., 1950. Determination of the ionic exchange during nervous activity by activation analysis. *Nature*, Vol. 165, pp. 809–10.

King, W. B. R., 1950. Floor of the English Channel. *Geolog. Mag.*, Vol. 87, pp. 383–4.

Lebour, M. V., 1950. Some Euphausids from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 119, pp. 823–37.

Lebour, M. V., 1950. Notes on some larval Decapods (Crustacea) from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 120, pp. 369–79.

Lebour, M. V., 1951. Notes on some larval decapods (Crustacea) from Bermuda. II. *Proc. Zool. Soc. Lond.*, Vol. 120, pp. 743–7.

Lowndes, A. G., 1950. The males of *Canthocamptus bidens* Schmeil. *Proc. Zool. Soc. Lond.*, Vol. 120, pp. 395–403.

Menon, M. D. (with an appendix by T. J. Hart), 1950. The use of bones, other than otoliths, in determining the age and growth-rate of fishes. *Journ. du Conseil*, Vol. 16, pp. 311–35, appendix pp. 335–40.

Nicol, J. A. C., 1950. Autonomic nervous system of the ratfish. *Nature*, Vol. 165, p. 854.

Nicol, J. A. C., 1950. The autonomic nervous system of the Chimaeroid fish *Hydrolagus colliei*. *Quart. Journ. Micr. Sci.*, Vol. 91, pp. 379–99.

Russell, F. S., 1950. Hydromedusae—Family: Tubulariidae (contd.). Family: Margelopsidae. *Cons. Internat. Explor. Mer, Zooplancton.* Sheet 28.

Russell, F. S., 1950. Hydromedusae—Family: Corynidae. *Cons. Internat. Explor. Mer, Zooplancton.* Sheet 29.

Steven, G. A., 1950. Swimming of dolphins. *Sci. Progress*, Vol. 151, pp. 524–5.

Steven, G. A., 1950. *Nets. How to Make, Mend and Preserve them.* 128 pp. London: Routledge and Kegan Paul.

### Membership of the Association

The total number of members on 31 March 1951 was 612, being 69 more than on 31 March 1950; of these the number of life members was 80 and of annual members 532. The number of Associate members is now six, Mr A. T. A. Dobson, C.B., C.V.O., C.B.E., having been elected during the year.

### Finance

*General Fund.* The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

*Private Income.* The Council gratefully acknowledge the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£20), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Sheffield (£10. 10*s*.), Nottingham (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), Hull (£10. 10*s*.), Southampton (£10. 10*s*.), and the Imperial College of Science and Technology (£10).

## President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1951–52:

*President*

Prof. James Gray, C.B.E., M.C., Sc.D., LL.D., F.R.S.

*Vice-Presidents*

The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholàs E. Waterhouse, K.B.E.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
The Rt. Hon. Tom Williams, M.P.
G. P. Bidder, Sc.D.
W. T. Calman, C.B., D.Sc., F.R.S.
Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S.
E. S. Russell, O.B.E., D.Sc.
Sir Edward J. Salisbury, Kt., C.B.E., D.Sc., Sec.R.S.
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.
A. T. A. Dobson, C.B., C.V.O., C.B.E.
Major E. G. Christie-Miller
Morley H. Neale

## COUNCIL

*To retire in 1952*

Michael Graham, O.B.E.
C. E. Lucas, D.Sc.
L. Harrison Matthews, Sc.D.
J. D. H. Wiseman, Ph.D.
Prof. V. C. Wynne-Edwards

*To retire in 1953*

G. E. R. Deacon, D.Sc., F.R.S.
E. Ford
F. C. Fraser, D.Sc.
Prof. J. E. Harris, Ph.D.
Prof. C. M. Yonge, D.Sc., F.R.S.

*To retire in 1954*

J. S. Colman
H. Cary Gilson
Prof. Alastair Graham, D.Sc.
N. A. Mackintosh, C.B.E., D.Sc.
Prof. J. Z. Young, F.R.S.

*Hon. Treasurer*

Major E. G. Christie-Miller, 38 Hyde Park Street, London, W. 2

*Secretary*

F. S. Russell, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
H. J. Johns, C.B., M.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Major E. G. Christie-Miller
  Harrison S. Edwards
Prof. A. C. Hardy, D.Sc., F.R.S. (Oxford University)
Prof. J. E. Smith, Ph.D. (Cambridge University)
E. Hindle, Sc.D., F.R.S. (British Association)
H. W. Parker, D.Sc. (Zoological Society)
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

## BALANCE SHEET 31ST MARCH 1951

| 31st March 1950 | | | £ | £ |
|---|---|---|---|---|
| | CAPITAL RESERVE ACCOUNT: | | | |
| 32,688 | As at 31st March 1950 ... ... ... ... ... | | | 32,688 |
| | SURPLUS ACCOUNT: | | | |
| | As at 31st March 1950 ... ... ... ... ... | | 4,680 | |
| 4,680 | *Add:* Excess of Income over Expenditure for the year | | 2,223 | |
| | | | | 6,903 |
| 37,368 | | | | 39,591 |
| | AQUARIUM SINKING FUND: | | | |
| | As at 31st March 1950 ... ... ... ... ... | | 196 | |
| | *Add:* Donations for rebuilding Aquarium Tanks ... | | 28 | |
| 196 | | | | 224 |
| | E. T. BROWNE BEQUEST FUNDS: | £ | | |
| | Building Fund, as at 31st March 1950 ... | 25 | | |
| | *Less:* Expenditure on Extension of Workshops | 25 | | |
| | | | — | |
| | Library Fund, as at 31st March 1950... ... | 1,154 | | |
| | *Add:* Interest on Investment ... ... ... | 35 | | |
| | | | 1,189 | |
| | Special Apparatus Fund, as at 31st March 1950 | 2,510 | | |
| | *Add:* Interest on Investment ... ... ... | 77 | | |
| | | | 2,587 | |
| | Scientific Publications Fund, as at 31st March 1950 ... ... ... ... ... ... | 2,105 | | |
| | *Add:* Interest on Investment ... ... ... | 64 | | |
| | | | 2,169 | |
| 5,794 | | | | 5,945 |
| | COMPOSITION FEES FUND: | | | |
| | As at 31st March 1950 ... ... ... ... | | 762 | |
| | *Add:* Fees received during year ... ... | | 95 | |
| 762 | | | | 857 |
| | BUILDINGS RECONSTRUCTION FUND: | | | |
| | As at 31st March 1950 ... ... ... ... | | 426 | |
| | *Add:* War Damage Compensation received during year ... ... ... ... | 540 | | |
| | Estimated War Damage Compensation receivable (per contra)... ... ... | 1,000 | | |
| | | | 1,540 | |
| | | | 1,966 | |
| | *Less:* Expenditure during year | | | |
| | Buildings reconstruction ... ... | 1,181 | | |
| | Rebuilding East Wing... ... ... | 515 | | |
| | Equipment for East Wing ... ... | 94 | | |
| | | | 1,790 | |
| 426 | | | | 176 |
| | SUNDRY CREDITORS: | | | |
| 1,051 | Accrued Expenses ... ... ... ... ... ... | | 890 | |
| 183 | Subscriptions and Grant received in advance ... | | 180 | |
| | | | | 1,070 |
| | BANK OVERDRAFT: | | | |
| | Coutts & Co., London ... ... ... ... ... | | | 776 |
| £45,780 | | | | £48,639 |

| 31st March 1950 | | £ | £ |
|---|---|---|---|
| | FIXED ASSETS, at valuations as estimated by the Director at 31st March 1951: | | |
| | Boats and Equipment: | | |
| 11,000 | F.V. 'Sula' ... ... ... ... ... ... | 11,000 | |
| 200 | Motor Boat 'Gammarus' ... ... ... ... | 200 | |
| 100 | Nets, Gear and General Equipment ... ... | 100 | |
| 11,300 | | 11,300 | |
| 7,342 | Laboratory Apparatus, Equipment and Machinery ... | 8,851 | |
| | Library at valuation of Mr Ridgill Trout in January 1941, plus additions at cost ... ... ... ... | 17,887 | |
| 35,829 | | | 38,038 |
| | STOCKS ON HAND as valued by the Director: | | |
| | Specimens ... ... ... ... ... ... | 600 | |
| | Chemicals ... ... ... ... ... ... | 250 | |
| | Journals ... ... ... ... ... ... | 400 | |
| 1,250 | | | 1,250 |
| 232 | GENERAL FUND INVESTMENT at Book Value £352. 2*s.* 3*d.* 2½% Treasury Stock ... ... ... ... (Market Value £237. 13*s.* 6*d.* Last year £239. 8*s.* 9*d.*) | | 232 |
| 5,795 | E. T. BROWNE BEQUEST FUND INVESTMENTS, at cost £5901. 8*s.* 7*d.* British Transport 3% Guaranteed Stock 1978/88 ... ... ... ... ... ... (Market Value £5,222. 15*s.* 4*d.* Last year £5,252. 5*s.* 3*d.*) | | 5,795 |
| | COMPOSITION FEES FUND INVESTMENTS, at cost: | | |
| | £18. 8*s.* 6*d.* 2½% Treasury Stock ... ... ... | 16 | |
| | £872. 4*s.* 9*d.* British Transport 3% Guaranteed Stock 1978/88 ... ... ... ... ... ... | 841 | |
| 731 | (Market Value £784. 7*s.* 4*d.* Last year £662. 15*s.* 2*d.*) | | 857 |
| | SUNDRY DEBTORS: | | |
| 739 | Sale of Specimens, etc. ... ... ... ... ... | 785 | |
| — | War Damage Commission—Estimated compensation receivable (per contra) ... ... ... ... | 1,000 | |
| | | | 1,785 |
| 104 | PREPAYMENTS ... ... ... ... ... ... | | 89 |
| | BALANCE AT BANK AND CASH IN HAND: | | |
| | Lloyds Bank Ltd., Plymouth ... ... ... ... | 519 | |
| | Cash in Hand ... ... ... ... ... ... | 74 | |
| 1,100 | | | 593 |
| £45,780 | | | £48,639 |

*Note:* The Association had a capital commitment at 31st March 1951, in respect of a new building amounting to £2,200 which will be recoverable under a Treasury Grant.

JOHN E. HARRIS } *Members of the Council*
O. D. HUNT }

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion and to the best of our information and according to the explanations given to us, the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31st March 1951, and of the excess of income over expenditure for the year ended on that date.

We have obtained all the information and explanations which to the best of our knowledge and belief were necessary for our audit. In our opinion the Association has kept proper books of account and the above mentioned accounts, which are in agreement therewith, give in the prescribed manner the information required by the Companies Act, 1948.

*57 York Street, Plymouth.*
16 May 1951.

PRICE, WATERHOUSE & CO.
*Chartered Accountants*

## INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1951

| 31st March 1950 | | | £ | £ |
|---|---|---|---|---|
| *15,558* | SALARIES, including Association's contributions to Superannuation Scheme and National Insurance ... ... | | | 17,275 |
| *12,786* | LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance ... ... ... ... ... ... | | | 12,828 |
| *584* | UPKEEP OF LIBRARY ... ... ... ... ... | | | 765 |
| | SCIENTIFIC PUBLICATIONS, *less* sales ... ... ... | | 1,743 | |
| | *Less:* Grant from Dr M. Knight ... ... | 30 | | |
| | Grant from Birkbeck College ... ... | 7 | | |
| | | | 37 | |
| *1,202* | | | | 1,706 |
| | UPKEEP OF LABORATORIES AND AQUARIUM: | | | |
| *785* | Buildings and Machinery ... ... ... ... | | 479 | |
| *556* | Electricity, Oil, Gas, Coal and Water ... ... ... | | 651 | |
| *918* | Chemicals and Apparatus ... ... ... ... | | 1,159 | |
| *135* | Insurances, Tithe, Ground Rent and Rent of Store ... | | 136 | |
| *589* | Travelling Expenses ... ... ... ... ... ... | | 587 | |
| *10* | Audit Fees (2 years) ... ... ... ... ... | | 74 | |
| *577* | Stationery, Postages, Telephone, Carriage and Sundries | | 764 | |
| *180* | Specimens ... ... ... ... ... ... ... | | 207 | |
| | | | | 4,057 |
| | MAINTENANCE AND HIRE OF BOATS: | | | |
| *605* | Petrol, Oil, Paraffin, etc. ... ... ... ... | | 633 | |
| *1,884* | Maintenance and Repairs to Nets, Gear and Apparatus | | 1,486 | |
| *143* | Boat Hire, Collecting Expenses and Upkeep of Truck | | 224 | |
| *668* | Insurances ... ... ... ... ... ... | | 690 | |
| *1,380* | Hire of R.V. 'Sabella' ... ... ... ... ... | | 1,380 | |
| | | | | 4,413 |
| *33* | ENTERTAINMENT EXPENSES ... ... ... ... | | | 40 |
| *27* | BANK CHARGES ... ... ... ... ... ... | | | 35 |
| *2,218* | BALANCE, being Excess of Income over Expenditure for the year ... ... ... ... ... ... ... | | | 2,223 |
| | *Note:* No provision is made for replacement of Fixed Assets. | | | |
| *£40,838* | | | | £43,342 |

| 31st March 1950 | | | £ | £ |
|---|---|---|---|---|
| | GRANTS AND TABLE RENTS: | | | |
| *34,000* | Ministry of Agriculture and Fisheries grant from Development Fund ... ... ... ... ... | | 36,350 | |
| *500* | Fishmongers' Company ... ... ... ... | | 500 | |
| *1,276* | Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s.* 0*d.*, Leeds £20, Durham £10. 10*s.* 0*d.*, Exeter £10. 10*s.* 0*d.*, Leicester £10. 10*s.* 0*d.*, Manchester £10. 10*s.* 0*d.*, Nottingham £10. 10*s.* 0*d.*, Southampton £10. 10*s.* 0*d.*, Hull £10. 10*s.* 0*d.*, Sheffield £10. 10*s.* 0*d.*, Imperial College £10, and Ministry of Works £104.) ... | | 1,273 | |
| | | | | 38,123 |
| *473* | SUBSCRIPTIONS (excluding subscriptions received in advance) ... ... ... ... ... ... ... | | | 514 |
| *12* | FEES FOR TESTS OF MATERIALS ... ... ... ... | | | 65 |
| | SALES: | | | |
| *2,521* | Specimens ... ... ... ... ... ... | | 2,350 | |
| *361* | Fish ... ... ... ... ... ... ... | | 410 | |
| | Nets, Gear and Hydrographical Apparatus ... | 1,922 | | |
| | *Less:* Cost of Materials ... ... ... | 1,494 | | |
| *225* | | | 428 | |
| | | | | 3,188 |
| *29* | INTEREST ON INVESTMENTS ... ... ... ... | | | 31 |
| *8* | SALES OF DR M. V. LEBOUR'S BOOK ... ... ... | | | 6 |
| *9* | SALES OF 'PLYMOUTH MARINE FAUNA' ... ... ... | | | 7 |
| | AQUARIUM: | | | |
| | Admission Fees ... ... ... ... ... ... | | 1,601 | |
| | Sales of Guides and Postcards ... ... ... ... | | 108 | |
| | | | 1,709 | |
| | *Less:* Maintenance of Building... ... ... | 52 | | |
| | Printing Tickets and Guides ... ... | 47 | | |
| | Food ... ... ... ... ... ... | 105 | | |
| | Wages ... ... ... ... ... ... | 97 | | |
| | | | 301 | |
| *1,424* | | | | 1,408 |
| *£40,838* | | | | £43,342 |

# STUDIES ON *CHAETOPTERUS VARIOPEDATUS* (RENIER). I. THE LIGHT-PRODUCING GLANDS

By J. A. Colin Nicol
Zoologist at the Plymouth Laboratory

(Plates I, II and Text-figs. 1–4)

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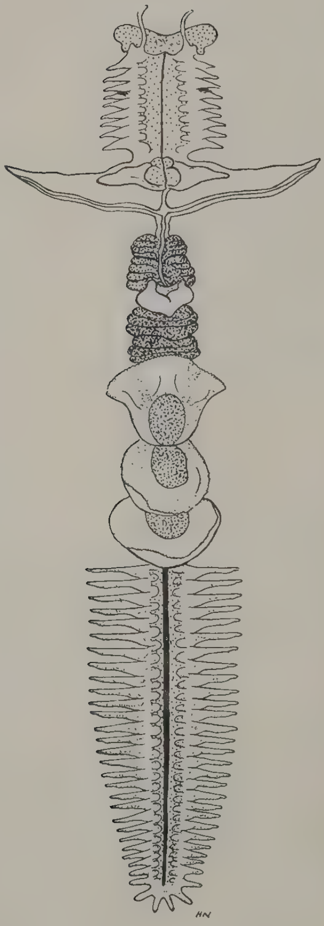
## INTRODUCTION

*Chaetopterus variopedatus* (Renier) is a tube-dwelling worm that has noteworthy luminescent powers. Production of light is by an extracellular process resulting from the discharge of a luminescent slime into the sea water. Because of its luminescent ability, the epidermal glands of *Chaetopterus* have been repeatedly described in detail, but it is still not clear what elements produce the luminescent secretion. I have, therefore, re-examined the histology of the light-producing regions of *Chaetopterus* with a view to determining the character of the photocytes or light-producing glandular cells.

For the convenience of the reader who may be unacquainted with the morphology of *Chaetopterus*, a picture of the animal is given in Text-fig. 1. *Chaetopterus* consists of three greatly dissimilar regions. The anterior region is flattened, and includes eleven segments (nine setigers). There is a pair of peristomial tentacles on the head. The middle region begins with segment XII, which is provided with a large pair of wing-like (aliform) notopodia. There is a lateral ciliated groove on the dorsal surface of each of these notopodia; the two lateral grooves converge medially, and open into a medial dorsal ciliated groove, which extends anteriorly towards the mouth. In the succeeding segments of the middle region there is a conspicuous cup organ (dorsal tubercle) in segment XIII, and a large fan or palette in each of segments XIV–XVI. The posterior region is less differentiated, and contains a large and variable number of segments, each provided with a pair of lateral notopodia.



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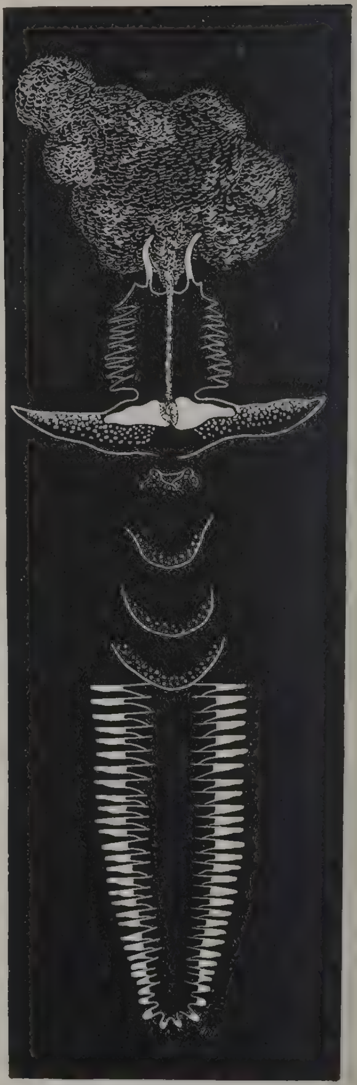

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Text-fig. 1. Dorsal view of a specimen of *Chaetopterus variopedatus*. About life-size.

Text-fig. 2. Dorsal view of a luminescing specimen of *Chaetopterus*, as seen in the dark. About life-size.

## HISTOLOGICAL METHODS

For the examination of glandular cells, material was fixed, double-embedded in Peterfi's celloidin-paraffin, sectioned at $10\,\mu$, and stained in various ways. Of several fixatives that were tried, Bouin's solution afforded good fixation and enhanced staining. After a trial of various stains it was concluded that a haematoxylin and eosin coloration afforded the greatest distinction between different gland cells and other epidermal elements, and most sections were stained by this means.

## REVIEW OF PREVIOUS WORK

It has been pointed out by several observers that the luminescent regions of *Chaetopterus* are recognizable in the living animal because of their chalky white appearance against the yellowish ground colour of the body. These whitish areas are considered to contain the glandular luminescent cells. These were mentioned by Joyeux-Laffuie (1890), who stated that unicellular gland cells with refringent contents were scattered over the luminescent regions. According to the descriptions of later histologists, the epidermal glandular cells are divisible into categories of granular or homogeneous eosinophile cells, fibrous eosinophile cells, and basophile cells.

*Granular and homogeneous eosinophile cells.* These are ovoid or flask-shaped cells containing a basal flattened nucleus, and opening directly to the exterior through a secretory pore. The cytoplasm contains numerous closely packed eosinophilic granules, which are sometimes fused to form a homogeneous mass. These cells occur all about the circumference of the peristomial tentacles, but particularly on the dorsal side; in an oval glandular area on either side of the dorsal ciliated groove in segment XII; on the dorsal surface of the aliform notopodia; in a lateral intermediate zone about the dorsal tubercle; in the walls of the fans; and along the notopodia of the posterior region (Krekel, 1920; Trojan, 1913). It is these cells, apparently, that Dahlgren (1916) regarded as luminescent cells or photocytes. He described them as saccular elements, hanging down from the cuticle, and capable of secreting granules of luminescent material. The discharged cells appear empty and shrunken (Harvey, 1920).

*Fibrous eosinophile cells.* These cells, according to Krekel (1920) and Trojan (1913, 1914), are found in the apical half of notopodia of the posterior region. They are cylindrical or fusiform in shape, with a basal nucleus. The cytoplasm is intensely acidophilic, and contains a peculiar fibrous skein or knot in the shape of a figure-of-eight. These cells had been noticed earlier by Claparède (1870), who designated them 'follicules bacillipares'. A developmental cycle has been traced in the history of these cells in which early stages are represented by ovoid elements possessing a granular cytoplasm. As the cells mature they elongate and extend to the base of the epidermis, and the contained cellular granules aggregate to form a spiral fibrous knot.

Trojan (1914) believes that these fibrous cells secrete the material used in tube-building.

*Basophile cells.* These cells occur in the following regions: (i) in the tentacles, where they are concentrated as a dorsal band; (ii) in the dorsal triangular glandular areas at the bases of the aliform notopodia; (iii) in the walls of the dorsal tubercle and fans of the middle region; (iv) in a distal band on the anterior side of posterior notopodia; and (v) in special glands at the base of these structures. The cells are pyriform to high cylindrical, and extend through the whole thickness of the epidermis. They become thinner distally, and open to the exterior through a secretory pore. The cellular contents consist of large basophilic granules staining intensely with haematoxylin, thionine and methylene blue; they are also coloured by mucicarmine (Krekel, 1920; Trojan, 1913). It is these cells which have generally been regarded as the photocytes producing the luminescent secretion, although Dahlgren (1916) apparently thought they were merely mucous cells.

Bonhomme (1943) has recently re-examined the histology of *Chaetopterus* gland cells in the aliform notopodia and dorsal tubercle. He found that the luminous organ consists of a high-folded epithelium containing tall prismatic cells. These have a lateral flattened nucleus, and open distally by a secretory pore. The cellular contents consist of a thin basophilic lacework, which Bonhomme regards as the residual framework remaining after secretion induced by the action of fixatives. On the margins of these glandular areas he located premucigenous cells which are large and irregularly prismatic in shape, and are filled with gross basophilic granules.

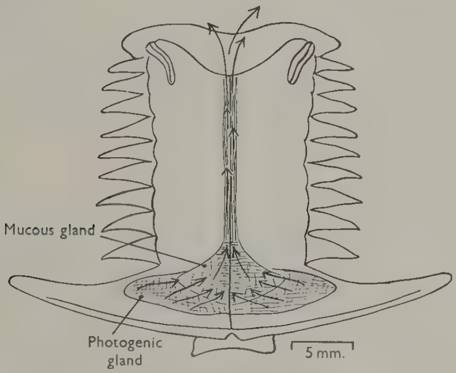
In another form, *Mesochaetopterus japonicus*, basophilic cells have also been identified with light production. These cells occur on the tentacles, on the dorsal surface of the middle region, and on the posterior notopodia. They are club-shaped, tapering towards a distal opening, and are filled with basophilic secretory granules. Discharged cells appear filled with a spongy coagulum (Fujiwara, 1935).

In the following account I present some new observations on the luminescent areas of *Chaetopterus*. My observations link the secretion of photogenic material with eosinophile cells. The other cell types are mucous cells, and basophilic cells which may be concerned with tube-building.

## OBSERVATIONS

The luminescent regions have been determined by stimulating the animal to produce light in the dark. Stimuli used have been high-frequency condenser discharges, above six per second, and an isotonic solution of KCl. Both these agencies cause widespread luminescence in the worm. The following regions produce light: the peristomial tentacles; a pair of triangular areas lying on the dorsal surfaces of the aliform notopodia (segment XII), one on either side of the dorsal ciliated groove; the aliform notopodia themselves; the walls of the dorsal tubercle; the fans in segments XIV–XVI; and all notopodia of the posterior region (Text-fig. 2).

The large glandular areas on the aliform notopodia are the regions most easily brought into luminescence by tactile stimulation. When this region is touched a luminescent secretion is discharged into the sea water; this is carried medially towards the mid-dorsal line by ciliary currents, and is then transported anteriorly towards the mouth through the activity of the dorsal ciliated groove (Text-fig. 3). Arriving in the buccal region, the luminescent secretion streams away from the animal, and illuminates the surrounding sea water. Luminescence from the secretion of this region persists for a considerable time, up to 15 min. or more. Under the binocular microscope the luminous secretion is revealed as a multitude of brightly lighted, discrete particles.



Text-fig. 3. Dorsal view of the anterior region and segment XII of *Chaetopterus*. The arrows indicate the course of luminous particles secreted by the luminescent glands at the bases of the aliform notopodia.

The other regions of the body give off a brief transitory flash, quickly dying away in a minute or two, and they do not discharge a luminescent secretion which is carried away into the surrounding medium. When segments of the posterior region are stimulated to lighten, the notopodia become coated or caked with a thick secretion which adheres for some time to the appendages. This secretion is probably the oxidized photogenic material, which luminesces and becomes exhausted very rapidly after it is released.

Bonhomme (1943) considers that the tentacles do not themselves give off light, but acquire luminescence secondarily when luminous secretion is carried forwards in the dorsal ciliated groove to a ciliated groove lying along each tentacle. This is incorrect, and the peristomial tentacles do lighten, as can be shown by the following experiment. The anterior region of an animal was transected at the level of the third or fourth segment, without inducing luminescence. The anterior fragment was then placed in isotonic KCl, upon which both tentacles luminesced. There was no question of luminescent secretion being carried to the tentacles from other regions in this fragment, and light originated in the tentacles themselves.

Trojan (1913) and Krekel (1920) regard a whitish glandular area at the base of each posterior notopodium as a luminescent structure, and Panceri (1878) figures this region as luminous. Krekel, unfortunately, did not have living animals for observation. There is a conspicuous whitish fleck at the base of each posterior notopodium, and I find that this region is not luminescent. Distally, beyond this whitish glandular area, the notopodium is brightly luminous.

## *Epidermal Gland Cells*

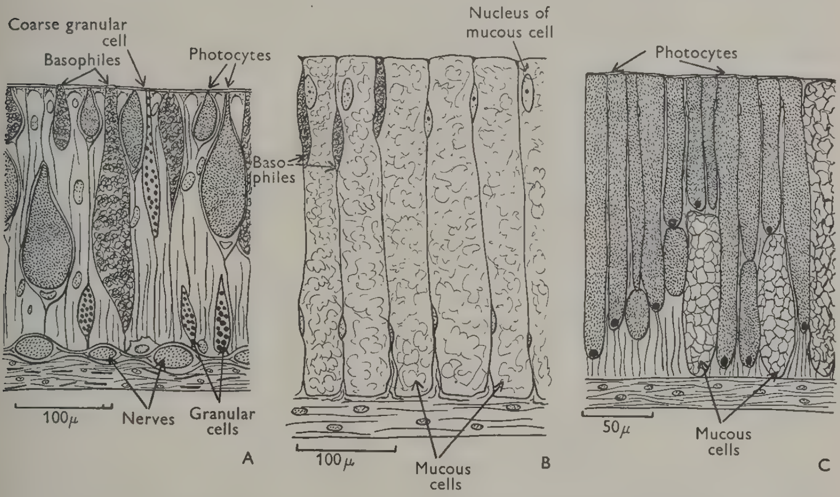
The story of epidermal secretions in *Chaetopterus* has obviously become rather complicated. In presenting an evaluation of these observations it is necessary to consider the probable functions of epidermal secretions in this species. So far as is known they involve production of mucus, tube-formation, and luminescence. One would, therefore, expect to find at least three kinds of epidermal gland cells corresponding to these functions, and such cells may or may not be visually distinguishable from one another.

### *Mucous Cells*

As is well known, *Chaetopterus* is a mucous filter-feeder and produces enormous quantities of mucus for trapping and entangling food particles as it pumps water through its tube (MacGinitie, 1939; MacGinitie & MacGinitie, 1949). This mucous material is poured forth from the walls of the dorsal tubercle and the aliform notopodia, and it is carried forward in the dorsal ciliated groove towards the mouth. There is little doubt that it is secreted by the abundant basophilic cells which form conspicuous whitish areas on those organs. Those cells are, accordingly, mucous cells.

The mucous glands occurring as conspicuous masses at the bases of the aliform and posterior notopodia and in the dorsal tubercle are made up of closely packed very large cells (Text-fig. 4; Pl. I, figs. 2–4 and 6). There is also a small number of mucous cells about the longitudinal ciliated groove on each peristomial tentacle. These are greatly elongated prisms about $20 \times 200\,\mu$ in the aliform notopodia, up to $350\,\mu$ long on the dorsal tubercle, and reaching the enormous length of $650\,\mu$ on the posterior notopodia. Nuclei are present at two levels in the mucous epithelium, and there is reasonable doubt as to which nuclei actually belong to the mucous cells. Towards the base of the epithelium there are small flattened nuclei squeezed between the mucous cells. These apparently belong to connective tissue cells located in a thin strand of connective tissue which extends a short distance between the bases of the mucous cells from the underlying fibrous layer. Distally toward the free surface, there are greatly elongated and faintly staining nuclei lying against the walls of the cells. These correspond to the nuclei figured by Bonhomme, and seem to be the nuclei of the mucous cells. Cell boundaries are faint but definite. The entire cell is filled with an indistinct alveolar material, the walls of the alveoli seemingly consisting of interlacing fine fibrils. The contents stain faintly with alum haematoxylin and are basophilic. They do not stain with mucicarmine and iron haematoxylin.

The following observations should demonstrate that the mucous cells are not responsible for the luminescent secretion. The secretion of mucus from segments XII and XIII (aliform notopodia and dorsal tubercle) is a continuous process, whereas release of luminous material is a discontinuous process, under nervous control. It is difficult to conceive of a cellular organization by which an exocrine glandular cell produces and releases two different substances, one continuously, the other at rare intervals.



Text-fig. 4. A, section across the epidermis of the aliform notopodium. B, section through the mucous epithelium beside the dorsal ciliated groove. C, section through the light gland on the aliform notopodium.

The main argument for identifying the basophilic mucous cells with light production has been the exact spatial correspondence between areas containing these cells, and luminescence. As shown above, the three regions containing large accumulations of mucous cells are the dorsal triangular regions on the aliform notopodia, the walls of the dorsal tubercle, and the bases of the posterior notopodia. Only the first of these three areas produces conspicuous light; the tubercle gives off a very weak and transitory flash; and the basal areas of the posterior notopodia do not luminesce. Consequently, there is no correspondence between aggregations of mucous cells and luminescence.

In order to obtain some comparative data on the relative amounts of mucus produced by various regions of the body, fragments of animals were placed in sea water and, after an interval to allow for secretion, the viscosity of the water was estimated in arbitrary units. Pieces of the animal selected were the anterior region (including segment XII); segment XIII and the dorsal tubercle; segments XIV–XVI and fans; and the posterior region. These were placed in separate dishes, an equal amount of water was added to each container and a sample of water drawn after 30 min. Relative viscosity figures were obtained by measuring the time taken for a drop to run through a length of thistle tubing. Mean relative times were: 5·3 sec. for the anterior region; 1·0 sec. for the dorsal tubercle; 0·5 sec. for the fans; and 0·2 sec. for the posterior region. The last figure was equivalent to a determination for sea water. These figures show that most mucus is secreted by the aliform notopodia, a considerable quantity by the dorsal tubercle, and none by the posterior notopodia. In contrast, it may be mentioned again that although a great deal of light is produced by the aliform notopodia, very little originates in the dorsal tubercle; the posterior notopodia, however, are brightly luminescent.

The copious mucus secreted by the aliform notopodia and the dorsal tubercle forms a vehicle for suspending and carrying away the luminous material secreted by the aliform notopodia. The luminescent material released by the dorsal tubercle is negligible. The fact that the posterior notopodia do not produce mucus when the animal is stimulated to luminesce offers an explanation why the photogenic material continues to lie on the surface of the notopodia, and is not dispersed in the surrounding medium. The function of the basal glandular areas on the posterior notopodia remains obscure. These glands are regarded as the modified terminal regions of nephridial organs (Trojan, 1913). Since they are not luminescent they cannot be concerned with luminescence of eggs and larvae, a suggestion that has occasionally been adumbrated. There is a possibility, however, that they secrete only during spawning.

### *Eosinophilic Light Cells (Photocytes)*

These occur in the peristomial tentacles, basal dorsal surface of the aliform notopodia, distally on the aliform notopodia, dorsal tubercle, fans, and on the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 1–6, 7–8, 10–11).

On the tentacles the eosinophilic cells are scattered over the surface, and are more concentrated on one side opposite the longitudinal ciliated groove. The aliform notopodia contain occasional scattered eosinophile cells distributed over both dorsal and ventral surfaces away from the lateral ciliated groove. Towards the base of the aliform notopodium, on the dorsal surface, there is a dense and extensive aggregation of eosinophilic cells. These lie lateral to a more median area which consists of basophilic mucous cells, and which borders the dorsal ciliated groove. The two kinds of cells are not mutually exclusive for there are a few eosinophilic cells dispersed through the mucous gland, and a few mucous cells scattered through the eosinophile glandular area.

In the dorsal tubercle of the middle region there is a narrow zone containing a few eosinophile cells. This lies at the transition between the dense mucous glandular layer covering the outside of the tubercle, and the ciliated epithelium leading inside the cup. Eosinophile cells are scattered over the dorsal surface of the fans. In the posterior region, the distal surface of each notopodium contains a great number of closely spaced eosinophile cells.

The eosinophile light cells have a similar appearance in all regions of the body in which they occur. On the tentacles, aliform notopodia, dorsal tubercle, fans, and posterior notopodia, they are round or oval to elongate elliptical in shape, depending on the height of the epithelium. Dimensions in these regions lie in the range $12–25 \times 30–50\,\mu$. There is a small triangular nucleus at the base of the cell. The dense aggregations of eosinophilic cells lying at the bases of the aliform notopodia are tall cylindrical in shape, and have dimensions of $6 \times 150\,\mu$. The nucleus, again basal, is relatively minute compared with the size of the cell. These cells, at the bases of the aliform notopodia, reach the basement membrane. In other regions, however, the oval or elongate cell has the appearance of hanging down from the cuticle, and a long thin tag extends from the base of the cell to the basement membrane. The contents of all these cells are closely similar. The cells are filled with a deeply staining dense mass of eosinophilic material in which there are all gradations from a coarse or fine granular to a homogeneous consistency.

Dahlgren (1916), who has briefly dealt with the photocytes of *Chaetopterus*, describes them as granular cells. His figure seems to be a composite one, based on the structure of the eosinophile light cells described above, and the coarse eosinophile cells described in the next section.

The evidence for regarding these eosinophilic cells as the light-producing cells consists of the following observations. The eosinophilic cells have the same spatial distribution as the photogenic regions. The tentacles glow quite brightly, relative to their area, and contain many eosinophilic cells. Light production is very faint and transitory in the dorsal tubercle and fans, and relatively few eosinophilic cells are present on those structures. The distal regions of all the posterior notopodia luminesce very brightly, and these appendages are abundantly provided with eosinophilic cells. Regions that do not luminesce bear no eosinophile light cells having the characteristics described above.

Three animals were stimulated into luminescence by placing them in isotonic KCl for several minutes. The brightly luminous areas on the basal dorsal surface of the aliform notopodia were dissected out under a binocular microscope. These pieces of tissue were fixed, and were examined histologically. Two of them contained extensive patches of both basophilic mucous cells, and eosinophilic cells. The third consisted almost entirely of a dense aggregation of eosinophile cells (Pl. I, fig. 3).

An attempt was made to discriminate the photogenic cells by strongly stimulating the animal into luminescence, and then looking for secreting and exhausted cells. The results were ambiguous. Even after prolonged stimulation electrically or by treatment with KCl, it was still possible to elicit further luminescence by mechanical agitation of the glandular regions in segment XII. Histological examinations showed a certain amount of both mucous and eosinophilic material outside the cells, some exhausted eosinophilic cells, and numerous eosinophile cells still replete with secretory material. It appears to be difficult to exhaust all the luminescent cells by prolonged excitation.

It has been a common observation that dropping an animal into a fixative evokes luminescence. A bright flash is produced when an animal is dropped into fixatives like Bouin's, Zenker's, and Helly's fluids. If the animal is previously anaesthetized by immersion in isotonic $MgCl_2$ for 5–15 min., and is then placed in the fixative solution, it does not luminesce. These effects were utilized in searching for the luminescent gland cells. Animals, with and without previous treatment with $MgCl_2$, were dropped into fixative, and histological sections were prepared (Pl. II, figs. 7 and 8). Sections of animals that had been treated with $MgCl_2$ showed no secretion of eosinophile material. Sections of animals that had been dropped directly into fixative solutions showed many eosinophilic cells caught in the act of discharging a secretory mass from a distal cellular orifice, and a dense layer of eosinophilic secretion lying over the surface of the epidermis. Comparative examinations were restricted to the aliform notopodia, as being regions easiest to study.

Finally, dried smears were made of secretions from non-luminous and luminous animals. To do this some of the mucous slime from the dorsal surface of the anterior region was sucked up in a pipette and smeared on a slide. After drying, the smears were fixed in Bouin's fluid, and stained with haematoxylin and eosin. Smears from non-luminous animals showed only a small amount of dispersed basophilic mucous material. Smears from luminous animals showed, in addition, many particles of eosinophilic material scattered in the mucus, or aggregated into lumps. These particles were often in packets closely resembling the contents of eosinophilic cells (Pl. II, fig. 9).

### *Other Gland Cells*

Two additional types of epidermal gland cells must be mentioned. These are densely staining basophilic cells, and coarsely granular eosinophilic cells.

The dense basophilic cells were found scattered singly in the tentacles, on the aliform notopodia, in the walls of the fans, in the dorsal tubercle at the transition between mucous cells and the internal ciliated layer, and about the circumference of the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 4, 7–8 and 10). They are scattered infrequently between the mucous cells at the bases of the aliform notopodia and on the dorsal tubercle. To a greater or lesser degree they are dispersed over the ventral surface of segment XII, and in the epidermis of the anterior region.

These cells tend to be thin, elongated, and fusiform where the epithelium is high, and irregularly pyriform where the epithelium is low. Dimensions are 3–12 $\mu$ wide $\times$ 30–120 $\mu$ high. The nucleus is small and oval in shape, and lies at the base of the cell. The cell contents are basophilic and stain heavily with alum haematoxylin. They also selectively stain with mucicarmine. After Bouin fixation they have the appearance of a deeply staining alveolar meshwork of fine fibrils, with darkly stained points in the interstices of the meshes. The cells were sometimes seen in the act of secreting, when a slender tongue of secretory material projected through a narrow distal orifice. These darkly staining basophilic cells apparently have a widespread and general distribution over the epidermis. There is no evidence to show that they are in any way concerned with light production.

The coarse granular eosinophilic cells were noted about the circumference of the aliform notopodia, in the posterior notopodia, in the dorsal walls of the fans, and mixed with photocytes in the wall of the dorsal tubercle (Text-fig. 4; Pls. I and II, figs. 4–8, 10 and 11). They are also dispersed over the ventral surface of segment XII and in the epidermis of the anterior region. In shape they are frequently pyriform: the proximal portion is swollen and lies in the basal epidermal region, and a long neck extends up to the free surface. When not compressed by neighbouring glandular cells they are often elongate and cylindrical. Dimensions reach 15 $\times$ 180 $\mu$. There is a small, elliptical basal nucleus. The cell contains a number of scattered and discrete coarse granules up to 3 $\mu$ in size which are weakly eosinophilic. There is no evidence that these cells are related to the photocytes or that they are concerned in light production.

### *Epidermal Gland Cells and Tube-formation*

It has not been possible to confirm the existence of fibrous eosinophilic cells, concerned with tube-formation, in the posterior notopodia (Dahlgren, 1916; Trojan, 1914). It is suggested that the fibrous knots and skeins seen in the eosinophilic cells of the posterior notopodia by earlier observers were fixation artifacts resulting from localized condensations and swirls in the secretory contents of the eosinophilic photocytes. In addition, as previously mentioned, coarse eosinophile cells are also scattered over these appendages.

The functions of the dense basophilic and coarse eosinophilic cells lie outside the scope of this investigation since they are not involved in light production. It is suggested, however, that it would be of interest to investigate whether they are involved in tube-building. For comparison with the various gland cells, the staining reactions of the tube were investigated by peeling off thin strips and fixing in Bouin's fluid, so as to subject them to the same initial treatment as gland cells of the body wall. They were then stained with eosin, haematoxylin or mucicarmine. The preparations so obtained were found to have little affinity for eosin, but to stain deeply with haematoxylin; they were also coloured by mucicarmine. This provides suggestive evidence that the original secretion involved in tube-formation is basophilic, and implicates the dense basophilic cells, although it is not maintained that a correlation in staining affinities of this kind itself affords any conclusive proof. Presumably the material forming the tube is secreted in a fluid, or soft condition, and is moulded and hardened after release. Enders (1907) has studied the tube-building activities of *Chaetopterus*, and he describes how a worm enlarges its tube by splitting it longitudinally, and then produces a new strip of hardened 'mucus' to fill the gap. During this process the ventral lip is used to fashion and shape the new wall of the tube. The possibility should be considered that the coarse eosinophilic cells may also play some role in tube-formation, by hardening the material secreted for the formation of the tube, such as takes place during the secretion of the byssus in *Mytilus* (Brown, 1949).

## Conclusions

It has been shown in this investigation that four recognizably different kinds of gland cells can be seen in the epidermis of *Chaetopterus variopedatus*. These cells are all epicrine in nature in that they discharge their secretion to the external surface. They occur scattered individually over the surface, but are often aggregated into multicellular glands. These consist of groups of a few similar cells, or dense aggregations of cells which form massive glandular surfaces, as in the basal regions of the aliform notopodia. In the latter regions, also, the glandular surfaces are increased by folding of the epithelium.

The four kinds of glandular cells are readily distinguishable by their morphological appearance and staining characteristics. The photocytes, containing a densely staining eosinophilic mass, are confined to the luminescent regions. Mucous cells, containing a loose alveolar mucigen material, are aggregated into multicellular glands at the bases of the aliform notopodia, in the walls of the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell types, coarse granular eosinophilic and densely staining basophilic cells, are scattered singly through the epidermis and have a widespread distribution. Both these latter kinds of cells may be concerned with fabrication of the tube.

Only one kind of cell is implicated in light production in *Chaetopterus*, and this is of interest when compared with *Cypridina*. In the latter two separate cellular types are involved, one of which contains large yellow granules of luciferin, the other small colourless granules of luciferase. On release the granules dissolve in the water and interact to produce light. Corresponding to the absence of two recognizably different kinds of photogenic particles in *Chaetopterus* is the reported failure to isolate extracts of luciferin and luciferase from this worm (Harvey, 1926, 1940).

In a treatment of luminescence it is usual to make some reference to its function in the economy of the organism. The function of luminescence in *Chaetopterus* is still unknown. Dahlgren (1916) has reproduced a painting by Horsfall in which an eel is depicted as attacking a brightly luminescent worm in its tube. The inference seems to be that the light has biological value in repelling the predator. Harvey (1920), however, has noted that light production by *Chaetopterus* would be of no avail, since an extracted worm cannot build a new tube. In presenting his theory that luminescence may sometimes have survival value to a species in attracting a predator of a predator, Burkenhead (1943) has utilized *Chaetopterus* as a theoretical example, in which luminescence excited as the result of an attack by an eel would attract, secondarily, an attack upon the eel by a dogfish. It may be significant that the anterior region of *Chaetopterus* is easily autotomized under stress and is readily regenerated, and it is this region of the worm which pours forth such an abundant luminous secretion. This suggests the idea of a sacrifice lure. Speculations of this kind obviously need to be checked by experiment and by observation of the living animal.

## SUMMARY

The luminescent regions of *Chaetopterus variopedatus* are shown to be: the peristomial tentacles, the aliform notopodia, the dorsal tubercle, fans, and notopodia of the posterior region. The brightest areas are glandular masses on the dorsal basal surfaces of the aliform notopodia and the distal surfaces of the posterior notopodia.

The photogenic glands on the aliform notopodia give off a luminescent secretion that is suspended in mucus and is dispersed into the surrounding sea water. Light from other regions is much more transitory, and the luminescent secretion is not dispersed.

Four kinds of gland cells occur in the epidermis. The photocytes have been identified as eosinophile cells containing a dense secretory mass. These cells are confined to the luminescent regions, and they are most abundant on the two most brightly luminescent areas, namely, distally on the posterior notopodia, and at the base of aliform notopodia. Mucous cells are slightly basophilic cells occurring beside the dorsal ciliated groove in segment XII, on the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell

types are coarse granular eosinophile cells, and darkly staining basophile cells. The latter two kinds of cells may be involved in tube-building.

Earlier work dealing with the epidermal glands of *Chaetopterus* is reviewed, and some comparisons are made with other forms.

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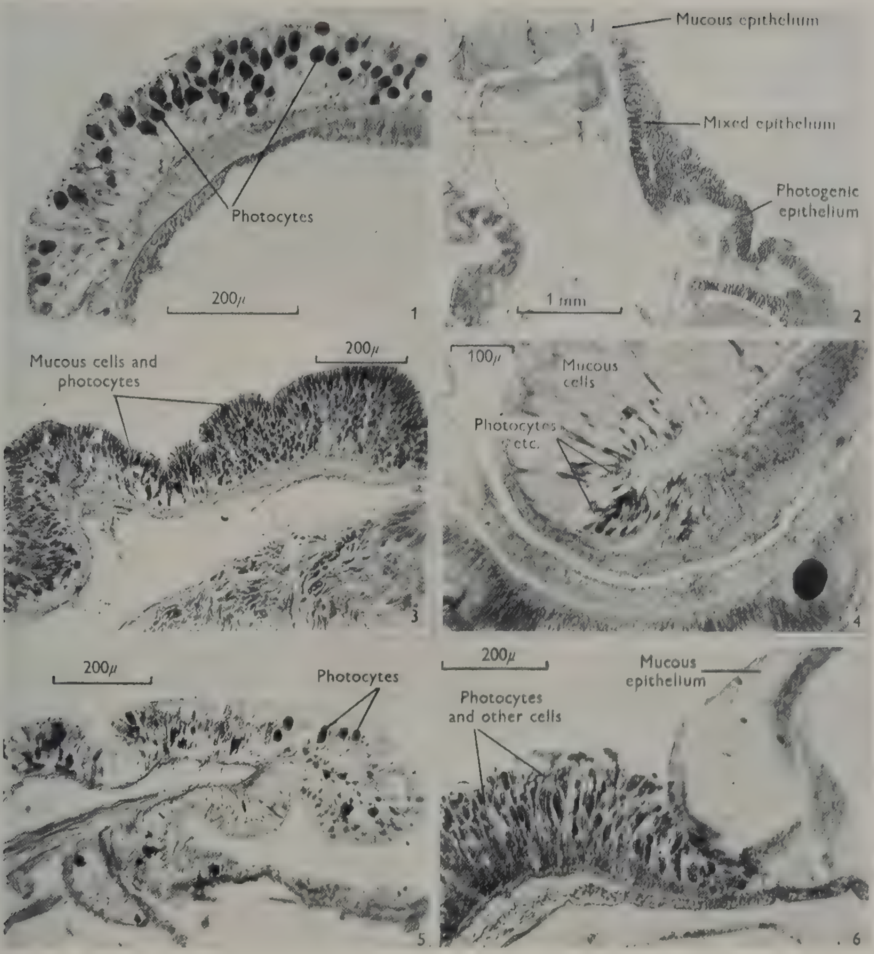
## EXPLANATION OF PLATES

### PLATE I

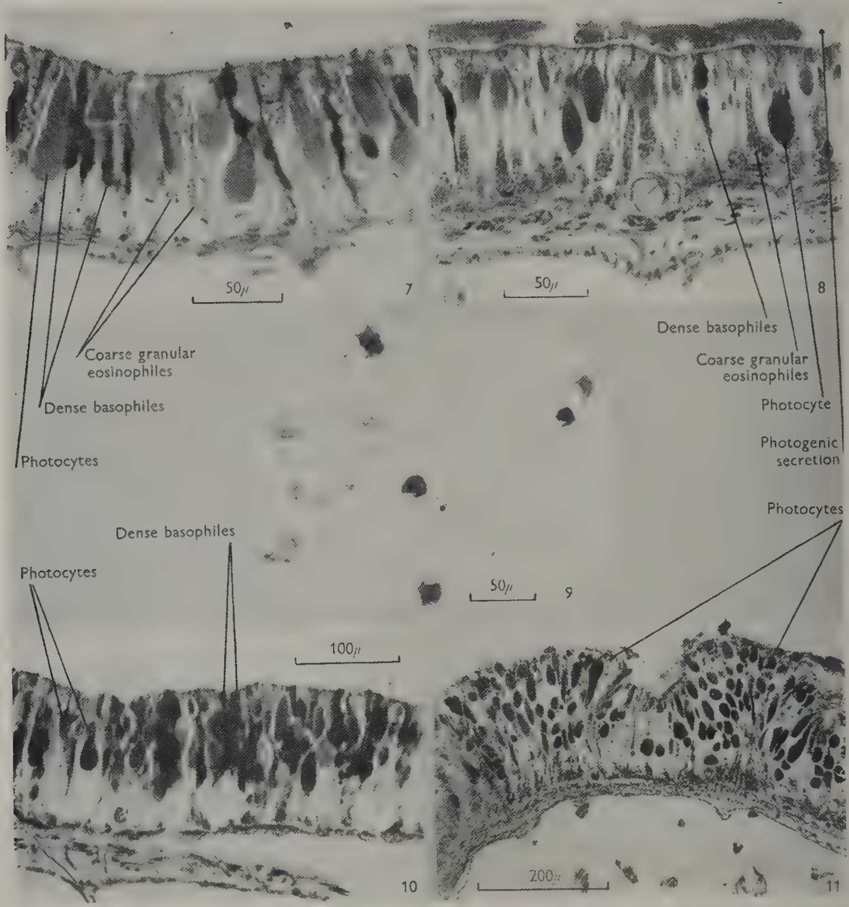
All histological sections shown in these photographs were stained with alum haematoxylin and eosin.

Fig. 1. Part of the wall of the peristomial tentacle in transverse section. Mucous cells and photocytes are interspersed in the epithelium.

Fig. 2. Transverse section through the dorsal body wall in segment XII. Lateral to the dorsal ciliated groove is a thick layer of mucous cells, which is replaced more laterally by a dense aggregation of photocytes.


Photocytes
200μ
1
Mucous epithelium
Mixed epithelium
Photogenic epithelium
1 mm
2
Mucous cells and photocytes
200μ
3
100μ
Mucous cells
Photocytes etc.
4
200μ
Photocytes
5
200μ
Mucous epithelium
Photocytes and other cells
6

Figs. 1–6.


50μ
7
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Coarse granular eosinophiles
Dense basophiles
Photocytes
Dense basophiles
Coarse granular eosinophiles
Photocyte
Photogenic secretion
Photocytes
Dense basophiles
Photocytes
50μ
9
100μ
10
200μ
11

Figs. 7–11.

Fig. 3. Dissected and isolated luminescent glandular epithelium from segment XII. The epidermis consists mostly of photocytes, with a few mucous cells.

Fig. 4. Transverse section of the dorsal tubercle at the junction of the mucous layer, and the ciliated surface. Mixed together at the junctional zones are photocytes, coarse granular eosinophile cells, and dense basophile cells.

Fig. 5. Transverse section of a fan. The epidermis contains a few photocytes, coarse granular eosinophile cells, and dense basophile cells.

Fig. 6. Longitudinal section of a posterior notopodium. Junction between the basal mucous gland (right) and the brightly luminescent epithelium (left). The light-producing epithelium to the left contains predominantly photocytes mixed with some coarse eosinophiles and a few basophiles.

### PLATE II

Fig. 7. Section of the aliform notopodium from a specimen anaesthetized with $MgCl_2$ before fixation. Surface secretion is lacking. Photocytes, coarse eosinophiles, and dense basophiles are interspersed together.

Fig. 8. Section of the aliform notopodium from a specimen fixed without preliminary anaesthetization. A layer of eosinophilic secretion lies over the surface of the epidermis. Photocytes, coarse eosinophiles, and a few dense basophiles lie interspersed together in the epithelium. A nerve is shown in section at the base of the epithelium.

Fig. 9. Dry smear of luminescent secretion produced by segment XII. Eosinophile secretory particles are shown.

Fig. 10. Section across the aliform notopodium to show dense aggregation of photocytes and dense basophilic cells.

Fig. 11. Section across the distal region of a posterior notopodium. The epidermis contains a dense aggregation of photocytes, together with a few coarse eosinophiles and dense basophiles.

# STUDIES ON *CHAETOPTERUS VARIOPEDATUS* (RENIER).

# II. NERVOUS CONTROL OF LIGHT PRODUCTION

By J. A. Colin Nicol

Zoologist at the Plymouth Laboratory

(Text-figs. 1–9)

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The production or emission of light is under nervous control in many marine animals that have a differentiated nervous system. The nature of this control is a field of neuro-effector physiology that has been little explored, but one which could advance considerably our knowledge of the behaviour and functioning of luminescent marine animals. Nervous control of luminescence is achieved in diverse ways in different animals, namely, by squeezing forth a pre-formed secretion through muscular contraction, as appears to take place in *Cypridina*; by exposing a continuously luminescent organ through rotation or by movement of shutters, as in the teleosts *Photoblepharon* and *Anomalops*; by initiating cellular changes that lead to intracellular luminescence, for example in the photophores of the shrimp *Acanthephyra debilis*; and by directly activating light gland cells to secrete. The last method is a special example of nervous regulation of glandular secretion, and is the process occurring in the polychaete *Chaetopterus* (Dahlgren, 1916; Harvey, 1920, 1940).

*Chaetopterus* has long been known as one of the more brilliantly luminescent marine invertebrates, and several previous workers have investigated this animal and reported on certain features of light production. This work is summarized to form a background for the original observations that follow.

## REVIEW OF PREVIOUS WORK

The luminous areas have been described and figured in a previous paper (Nicol, 1952). These are the peristomial tentacles, the surfaces of the aliform notopodia, a pair of photogenic glands on the dorsal basal surfaces of the aliform notopodia, the dorsal tubercle, fans, and notopodia of the posterior region. The luminous secretion produced by the photogenic glands on the aliform notopodia is suspended in mucus, and is carried away by ciliary currents to be distributed in the surrounding sea water. Luminescence in other regions is more transitory and localized (Bonhomme, 1943; Dahlgren, 1916; Fauvel, 1927; Joyeux-Laffuie, 1890; Lespès, 1872; McIntosh, 1915; Mangold, 1910–14; Panceri, 1878; Trojan, 1913, 1914; Will, 1844).

The light is blue in colour and has been shown by Lankester (1868) to have a continuous spectrum from about 440 to 530 m$\mu$.

Light is produced in *C. variopedatus* only as the result of stimulation. The stimuli used to excite this worm, and indeed most other marine animals investigated experimentally, seem to have been selected randomly, in order to determine whether or not they were effective, rather than to reveal the mechanism of the response. It was observed that mechanical stimulation, such as results from disturbing the animal on removing it from its tube, or pinching or tapping it, causes the production of light. Effective chemical stimuli which have been used include the application of fresh water and strong reagents such as sublimate, formol and other fixing fluids. Raising the temperature of the sea water and applying electrical currents have also been employed to induce luminescence (Dahlgren, 1916; Joyeux-Laffuie, 1890; Panceri, 1878; Trojan, 1913).

There is a general belief that light production in *C. variopedatus* is under nervous control, but a curious absence of agreement about the details of the process. Panceri (1878) observed that the production of light was confined to the region of stimulation, and that there was no transmission of excitation, and this has been confirmed by Trojan (1913). According to Hempelmann (1934), increasing the strength of the stimulus (kind ?) causes the light to spread to other parts of the body and to become more widely distributed, but Dahlgren (1916) ascribes this effect to the spread of secretion through the water. Again, Stephenson (1946) has stated that stroking the animal causes waves of light to pass over the body. Finally, Harvey has noted that the light cells are probably under nervous control 'as a strong stimulus in one part of the body causes luminescence which spreads over the whole surface of the worm' (1920), and 'a wave of light when the head end is stimulated' (1940). The luminous secretion remains bright for about a minute after stimulation ceases, and then gradually diminishes in intensity. It has also been noted that the luminescent cells fatigue rather readily, and after a period of mechanical stimulation a rest of some hours is required before the animal can be brought to luminesce again (Harvey, 1920; Panceri, 1878; Trojan, 1913).

There is agreement that luminescence is not inhibited by previous exposure to strong light. Panceri (1878) exposed specimens of *Chaetopterus* to sunlight, and then stimulated them in the dark, and he found that the ability to produce light was not suspended, in contrast to *Beroe* and other ctenophores in which such inhibition is quite pronounced (Panceri, 1872). According to Crozier (quoted by Harvey, 1920), luminescence in *Chaetopterus* is not affected by an exposure to 3000 metre-candles for 6 hr. The luminescent substances, luciferin and luciferase, which have been distinguished in marine ostracods, fire-flies (beetles), *Pholas* and *Odontosyllis*, have not been demonstrated in *Chaetopterus* (Dubois, 1887; Harvey, 1920, 1926, 1940, 1948). Neither do dried preparations of the animal luminesce on moistening. A luciferin-luciferase reaction may still be present, but may escape detection by biochemical methods hitherto employed. Harvey (1940) has reviewed this aspect of the subject.

Young free-swimming larvae of *Chaetopterus* are also capable of producing light (Dahlgren, 1916). Enders (1909), describing larvae about 1·5 cm. long and ready to metamorphose, states that luminosity is noticeable in the region of the ciliated rings, and in the mucus which the animals discharge. It is still more apparent in older larvae, where it appears in the anterior region and about the ciliated rings as the result of stimulation.

In another luminous chaetopterid, *Mesochaetopterus japonicus*, Fujiwara (1934, 1935) found that light is produced by the tentacles, by large areas of glandular epithelium on the dorsal surface of the first segment of the middle region, by a paired scyphiform organ on the second segment, by the dorsal ciliated region of the third segment of the middle region and by notopodia of the posterior region. These regions, in a general way, are similar to those of *Chaetopterus variopedatus*. Fujiwara's description (1935) of luminosity in this animal is difficult to follow. He states that brightest light is produced by the glandular epithelium of the first segment of the middle region, as in *Chaetopterus*. A luminescent secretion is also produced by cells in the walls of the dorsal ciliated groove, and the basal regions of the posterior notopodia are also luminous. He appears to imply that an animal removed from its tube shines continuously, but I interpret his account to mean that the luminescent secretion from the middle region of the body shines for some considerable time, but that light from notopodia of the posterior region, in contrast, appears in quick flashes. Moreover, the posterior segments flash alternately. Fujiwara further states that the luminescent activity can be increased by electrical, mechanical, or chemical stimulation. Electrical stimulation of the tentacles causes the appearance of light both in these structures, and in the luminescent organs of the posterior region. In *Mesochaetopterus japonicus*, therefore, it seems that excitation of luminescent organs, induced electrically, is transmitted by the nervous system throughout the length of the body; sensitivity to stimulation leading to a luminous response appears to be most pronounced in the tentacles.

## MATERIAL AND METHODS

Specimens of *Chaetopterus variopedatus* used in this investigation were maintained under circulation in the laboratory. Before use they were removed carefully from their tubes so as not to stimulate them to produce their luminous secretion before being experimented upon. This no doubt occurred on occasion, and any specimens which responded poorly to subsequent stimulation were discarded.

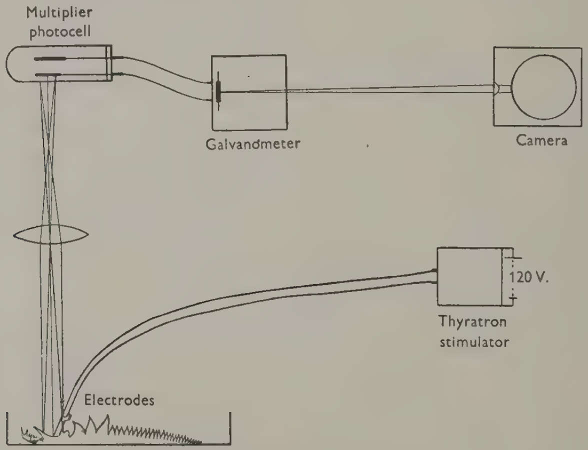

Fig. 1. Arrangement for investigating and recording luminescence, with the aid of a photocell and galvanometer.

Many of the experiments to be described merely depended on observing whether an animal did or did not luminesce, that is, whether the result was positive or negative. When it was necessary to obtain quantitative data, the light produced by the worm was focused on the photocathode of a photomultiplier cell (RCA 931 A). This was usually maintained at 1000 V., 100 V. per stage at which, according to specifications, it has a sensitivity of 3 A. per lumen and a magnification of $2 \times 10^5$ with a lamp of colour temperature 2870 K. The arrangement is shown in Fig. 1. As only comparative results within short time-periods were sought, no calibrations of the actual sensitivity of the cell were attempted. In most experiments the light from the basal glandular areas on segment XII only was measured. Photocurrent from the cell activated a moving-coil mirror galvanometer. This was a Tinsley instrument having a resistance of 337 Ω; deflexion of 130 mm./$\mu$A. at 2·16 m.; and a periodic time of 2 sec. Light reflected from the galvanometer mirror fell upon a sheet of moving bromide paper in a camera travelling with a speed of 6 mm./min. Two other spot-lights were thrown on the same paper, one a time marker flashing once per minute, the other a stimulus marker, flashing when the stimulus key was depressed.

There was perceptible dark current in all records, and some drift of dark current base-line. At the beginning and end of each experiment, and at appropriate intervening intervals, the animal was covered so as to record the level of dark current. Some galvanometer records have been replotted to allow for basic level of dark current, drift, and any initial luminescence upon which the effect of a specific stimulus was superimposed.

Success was also attained in recording photocurrent with an oscilloscope, and this method was used when it was desirable to obtain maximal sensitivity, and fast records showing the initial phases of the luminescent reaction. The apparatus employed was a double beam oscilloscope with d.c. amplifier and attached camera.

Other particulars about methods used are described later under appropriate headings.

## OBSERVATIONS

### *Effects of Mechanical Stimulation*

Mechanical stimulation, by pulling, pinching, or tapping the animal, causes luminescence. As other observers have noted, light is produced, in consequence, from the peristomial tentacles, edges of the aliform notopodia, cup organ or dorsal tubercle, edges of the fans and notopodia of the posterior region. The response to stimulation tends to be very localized: thus pinching a fan or the cup organ of the middle region results in a faint flash of light in the organ directly stimulated. Similarly, mechanical stimulation of the posterior region causes the appearance of light in a few parapodia in the area directly affected.

It is more difficult to determine the effect of mechanical stimulation on the aliform notopodia of the XIIth segment. Light appears on the borders of the aliform notopodia as the direct result of pinching or touching these structures, and sometimes in the basal glandular areas on the dorsal surface as well. Luminous secretion appears from the latter glands as the direct result of touching them, or indirectly from pulling on the animal so as to produce tension in that region. No luminescent secretion is produced in the XIIth segment as the result of tactile stimulation of other parts of the middle region, and of the anterior and posterior regions, as long as the XIIth segment itself is not disturbed. Strong mechancial stimulation of the glands at the bases of the aliform notopodia causes a profuse discharge of luminous slime. It is probable that actual cellular destruction as well as indirect nervous stimulation is involved in this display. As in other regions of the body, it appears from these results that the aliform notopodia and basal glands produce light only as the result of stimulation directly impinging on that segment. Light production in the aliform notopodia due to pulling or moving the animal seems to result from mechanical effects transmitted to the XIIth segment. There is, consequently, no definite evidence that mechanical stimulation in one region gives rise to a propagated excitation causing luminescence in more distant regions of the body. It is evident, however, that mechanical stimulation of *Chaetopterus* is very difficult to regulate quantitatively and spatially, and that more exact control can be exercised with electrical stimuli.

### *Effects of Electrical Stimulation*

Direct current, faradic stimulation, and condenser discharges all produce luminescence. Quantitative studies were confined to the use of condenser discharges from a thyratron stimulator, since they allow careful control of strength, duration and frequency. Stimuli were delivered through a pair of platinum electrodes laid on the surface of the animal.

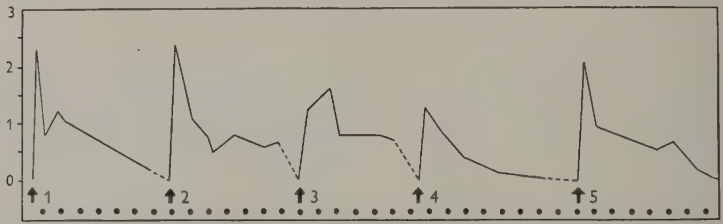

Fig. 2. Record of light produced by the photogenic glands on the aliform notopodia of *Chaetopterus* under electrical stimulation. Vertical arrows indicate application of stimuli. These were: 1 and 2, single stimuli; 3, two stimuli at 2 per sec.; 4, three stimuli at 3 per sec.; 5, one sec. burst at 5 per sec. Light intensity to the left in arbitrary units. Time scale below, 1 per min.

With the electrodes on the dorsal surface of the XIIth segment, a single electrical stimulus, above threshold, causes the production of luminescent secretion from the glands at the bases of the aliform notopodia (Fig. 2). The light appears quickly, within a few seconds of stimulation. Within a minute it begins to fade away, quickly at first, then more slowly, and becomes very dim and almost extinguished in 5 min.

The latent period and the time relations of the first phase of the luminescent response were determined from oscilloscope records (Fig. 3). In one series of experiments twenty animals were stimulated with a 2 sec. burst at 7 stimuli per sec. Latent periods measured from the beginning of stimulation varied from 3·0 to 4·4 sec., with a mean of 4·2 sec. The interval between first deflexion and maximal height on the records ranged from 3·4 to 24 sec., with a mean value of 10·3 sec. Measurements made by eye (light-adapted) and a stop-watch gave a mean latent period of 2·6 ± 1·8 sec. (minimal value 1·5 sec.). The eye is more sensitive than the photocell, and this figure would be reduced further by dark adaptation of the observer. Animals in the dark, therefore, would become visible in about 2 sec., and would attain maximal luminescence in about 12 sec. after stimulation, the exact times depending on the animal.

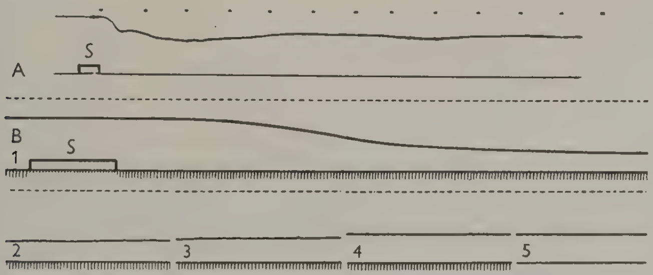

Fig. 3. Oscilloscope records of light produced by glands of aliform notopodia under electrical stimulation. A, 2 sec. burst of stimuli, at 9 per sec., at *S*. Time scale above, 1 per 5 sec. Latent period, 2·7 sec.; time to reach maximal intensity from first deflexion was 9·5 sec. B, 2 sec. burst at 14 per sec. at *S*. Time scale above, 1 per $\frac{1}{5}$ sec. There are 5 sec. intervals between 1–2, 2–3, 3–4, 4–5. Latent period, 3·6 sec.; time to reach maximal intensity from first deflexion was 11·4 sec.

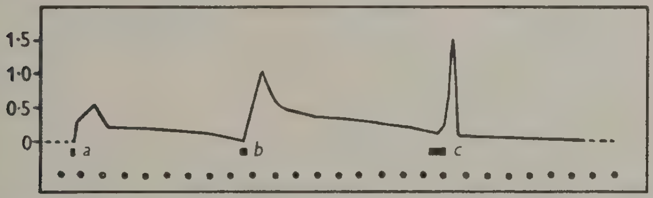

Fig. 4. Records of light produced by the photogenic glands on the aliform notopodia. Bursts of stimuli at 5 per sec. for 5 sec. at *a*, 30 sec. at *b*, and 1 min. at *c*. Stimulation indicated by dashes under record of light intensity. Time scale below, 1 per min.

The production of light by a single shock shows that there is a one-to-one relationship between single impulses and the light response: the arrival of an impulse at the neuro-effector junction excites the cell sufficiently to discharge. By increasing the number of stimuli, other factors, voltage and frequency, remaining constant, the light intensity and the amount of luminescent material secreted become greater. Fig. 4 is a record obtained in investigating this effect. Examination of the record shows that the initial luminescence increased greatly as the stimulation time was prolonged and the number of stimuli increased. With stimulation periods of 1:6:12, the maximal intensity of luminescence resulting was 1:2:3. The total amount of light produced lay in the ratio of about 1:2:0·6. Since the responses to the second and third bursts of stimuli were certainly diminished by a fatigue effect, the absolute luminescence which would have followed stimulation for a given period, if diminution due to previous stimulation were excluded, probably would have been much greater.

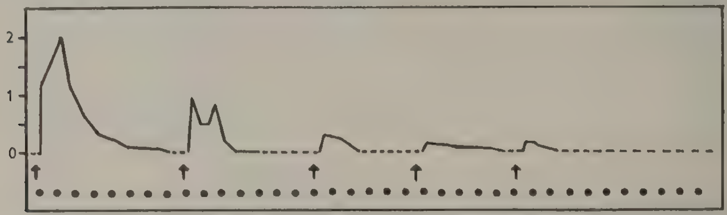

Fig. 5. Record of light produced by the photogenic glands on the aliform notopodia under repetitive electrical stimulation. Stimulation, indicated by vertical arrows under the light record, consisted of 5 sec. bursts at 8 per sec. except the last, which had a duration of 1 min. Time scale below, 1 per min. Intensity, to the left, in arbitrary units.

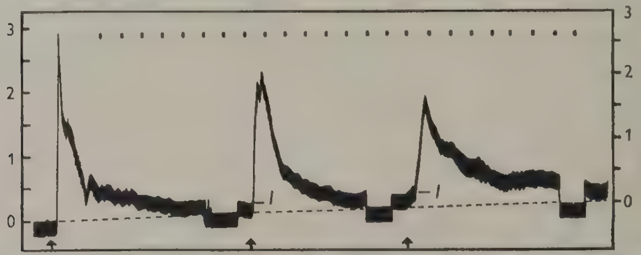

Fig. 6. Fatigue of luminescent power in the photogenic glands on the aliform notopodia. Stimulation, indicated by triangles below, 5 sec. periods at 4 per sec. The dotted line represents the level of dark current; *I*, indicates the initial level of residual luminescence on which a new response is superimposed. Time scale above, 1 per min. Light intensities to left and right in arbitrary units.

The light-producing glands soon fatigue on repeated stimulation, and this makes the interpretation of results more difficult. Information about the onset and course of fatigue was obtained by subjecting specimens to successive bursts of electrical stimuli. Figs. 5 and 6 show records obtained from two animals. In Fig. 5 the animal was stimulated by a succession of 5 sec. bursts at 8 per sec., except the last which lasted 1 min. An interval of about 6 min. between bursts permitted the luminescence to fade. It will be seen that each successive burst resulted in a fall in light production as the gland fatigued. Fig. 6 shows a similar result.

Recovery from fatigue was not observed in experimental animals. Fig. 7 shows the result of an experiment on an animal in which rest periods of

1 and 3 hr. intervened between successive periods of stimulation. In these times the response failed to recover to any extent, and much less luminescent material was secreted than at the beginning of the experiment. Other workers, however, have noted some recovery of luminescent ability after a rest period of several hours (see p. 434), but their observations were subjective. In any event, it is certainly a very slow process, and demonstrates that luminescence cannot function as a frequently repeatable event in the normal economy of this species.

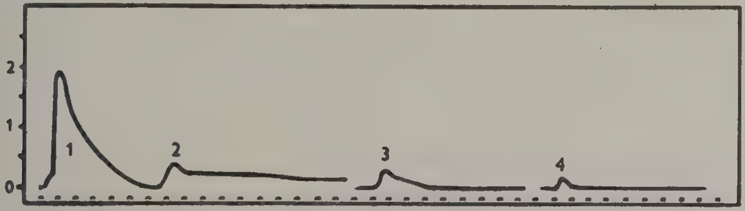

Fig. 7. Record of light produced by photogenic glands on the aliform notopodia. Fatigue in light-producing ability as the result of repeated electrical stimulation is demonstrated. 1, 2, 3, 4, light produced by 30 sec. periods of stimulation at a frequency of 2 per sec. Pause of 7 min. between 1 and 2; 1 hr. between 2 and 3; and 3 hr. between 3 and 4. Time scale below, 1 per min. Intensity, to the left, in arbitrary units.

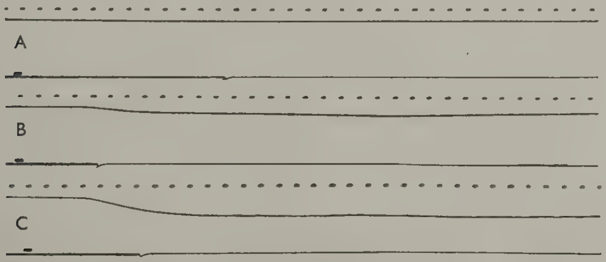

Fig. 8. Effect of voltage increases on the luminescent response. Oscilloscope records of light produced by the aliform notopodia. Stimulation consisted of 0·5 sec. bursts at 25 per sec., A, at 20 V., B, at 40 V., and C, at 60 V. Stimulation indicated below each record by a short horizontal line; time scale above each record, 1 per sec.

Gradually increasing the voltage, other factors remaining constant, increases the light response. Fig. 8 shows the result of an experiment in which the voltage was gradually increased, stepwise. For each rise in stimulus strength above threshold there is a corresponding increase in the resultant light intensity. The effect is probably due to the stimulation of more and more nerve fibres as the electric current becomes more widespread.

At a low frequency of stimulation (1·5 per sec.) light is confined to the region stimulated. Thus, when the stimulating electrodes are applied to the ventral surface of segment XII, against the nerve cord, and low frequency stimulation is applied, light appears in the aliform notopodia of that segment only. Stimulation of segments XIII, XIV, XV, or XVI, results in luminescence of the dorsal tubercle or fan in the segment stimulated (Fig. 9). Stimulation of the posterior region results in the appearance of light in a few (2–3) pairs of notopodia in the neighbourhood of the electrodes. Stimulation of segments anterior to XII at a low frequency has no effect. At a higher frequency, beginning at about 6 per sec., the excitation spreads to other segments, and the area affected increases as the frequency is raised. Thus, when the ventral surface of the posterior region is stimulated at frequencies of 6–9 per sec., the notopodia of about 10 posterior segments in the region of the electrodes luminesce. Further increase in frequency causes all notopodia of the posterior region to luminesce. Similarly, stimulation of the ventral surface of segments III–V at frequencies of 6 or more per sec. causes the aliform notopodia to luminesce. In some animals stimulation of the anterior region at high frequencies (9 or more per sec.) causes the excitation to be transmitted to middle and posterior regions of the body, as well. This was observed in only certain animals, however, and often excitation was confined to the anterior, middle, or posterior region, whichever was stimulated.

Transmission of excitation in these experiments is through the nerve cord. When the nerve cord is cut, and the animal is stimulated at a high frequency on one side of the incision, the excitation fails to jump the gap.

These observations point to the existence of internuncial facilitation in the nerve cord of *Chaetopterus*. The transmission of excitation from segment to segment presumably depends upon linked neurones arranged in series along the cord, and in connexion with this thesis it may be noted that giant axon systems are wanting in the nerve cord of *Chaetopterus*. In the nervous pathways involved in luminescence, single impulses, or impulses at low frequencies, are not transmitted from one neurone to the next along the cord. When the frequency is raised above a critical level, however, augmentation occurs at intervening synapses, and impulses can sweep through to successive segments.

### *Effects of Autonomic Drugs*

The cholinergic nature of the nerve fibres innervating certain glands in mammals is well established, and acetylcholine has been implicated as a chemical transmitter in the submaxillary and adrenal glands. Chemical transmitters have also been proposed in connexion with certain observations on neuro-muscular functioning of various annelids (Bacq, 1947; Botsford, 1941). It is of interest, therefore, to determine whether similar processes are involved in the nervous control of light production in *Chaetopterus*. Towards this end, the pharmacological effects of several autonomic drugs were tried on this animal.

The drugs employed were adrenaline, acetylcholine, nicotine, and eserine

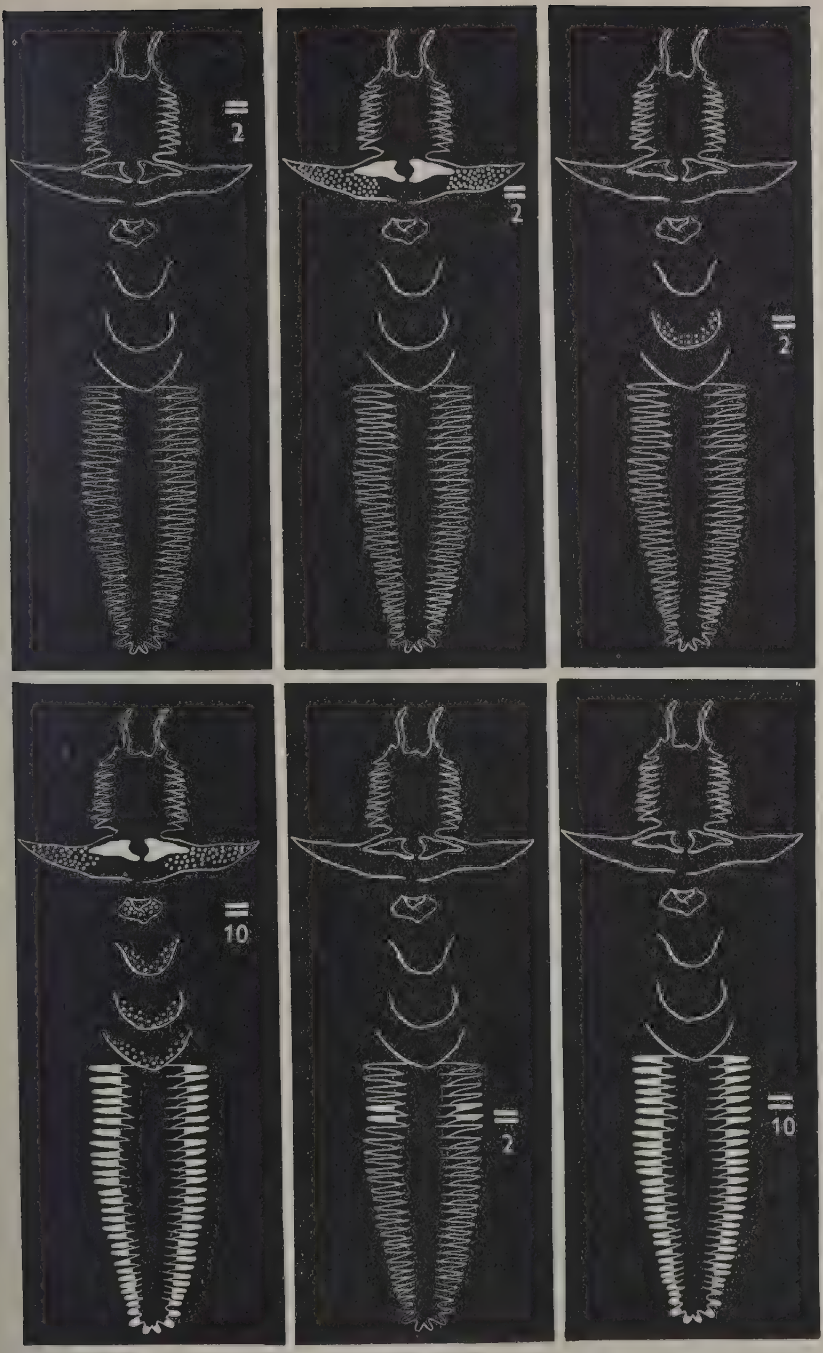

Fig. 9. The effects of stimulating the nerve cord at various frequencies. The double bar indicates the position of the stimulating electrodes. The numbers refer to the frequency of stimulation. Note the tendency for the excitation to spread as the frequency is raised.

(physostigmine salicylate). They were dissolved in sea water, in concentrations which are given as weight by volume, except for nicotine where the figures refer to concentrations in volume by volume. The solutions were applied in one of three ways: an intact animal was placed in a solution of the drug to be tested; or excised pieces of potentially luminescent tissues were placed in the solution; or solutions of drugs were injected into intact animals. The results of these experiments are summarized as follows.

*Adrenaline.* In concentrations of 1/1000 and 1/10,000 this drug failed to induce luminescence. This confirms an earlier observation of Harvey (1931) that adrenaline has no effect on luminescence in *Chaetopterus*.

*Acetylcholine.* Five intact animals were placed in a solution of acetylcholine (1/10,000), and one responded by luminescing brightly in all regions after intervals of 4–17 min., depending on the region lighting up. Injecting 0·1 or 0·2 c.c. of acetylcholine (1/100 to 1/5000) into the anterior or middle regions caused the appearance of flashes or persistent weak light in the fans, dorsal tubercle, and aliform notopodia. Pieces of the animal containing light-producing tissues and nerve cord shone feebly in solutions containing 1/1000 acetylcholine. Other pieces, from which the nerve cord was removed, behaved similarly.

*Eserine.* This drug had no apparent effect in concentrations of 1/1000 and 1/10,000.

*Eserine and Acetylcholine.* These two drugs, used together (both in concentrations of 1/1000 or 1/10,000) failed to evoke luminescence in isolated pieces of light-producing tissues. Injection of 0·2 c.c. of 1/1000 eserine and 1/1000 acetylcholine into the fans and anterior region resulted in some transitory flashes of light from the fans, dorsal tubercle, and aliform notopodia.

*Nicotine.* When tested on intact animals nicotine, in concentrations 1/1000 and 1/10,000, evoked a faint brief appearance of luminescence in about half the animals tested.

It is apparent from these results that sympathomimetic and parasympathomimetic drugs, which are frequently effective in inducing activity in other animals, have slight and rather inconsistent effects on light production in *Chaetopterus*. Acetylcholine and nicotine definitely induce luminescence in some animals, but the effect is somewhat irregular in occurrence and distribution. There is no evidence that eserine is effective by itself, or that it enhances the effect of acetylcholine in these experiments.

It is interesting that acetylcholine is effective in inducing luminescence in isolated pieces of light-producing tissues lacking central nervous system. This provides evidence that the drug is acting peripherally on the neuroglandular junction, although it does not exclude the possibility that it may be acting at other loci as well. The action of nicotine recalls its stimulatory effect on cholinergic neurones of other animals. The light produced by these drugs is usually rather weak and ephemeral, and probably reflects a slow rate of diffusion of the acetylcholine or nicotine through the tissues of the body wall. In general, it appears that acetylcholine exerts a nicotine-like action on the nervous system of this worm, and stimulates the neuro-effector junctions in the photogenic tissues.

Autonomic drugs have, of course, been used in the study of the luminescence of other animals. Adrenaline evokes the appearance of light in the photophores of the deep-sea fish *Echiostoma ctenobarba*, and of the midshipman *Porichthys notatus* from shallow waters (both teleosts) (Greene & Greene, 1924; Harvey, 1931, 1940). Adrenaline also produces a constant glow lasting several hours in the lampyrid *Photuris pennsylvanica* (Creighton, 1926; Emerson & Emerson, 1941.)

It is doubtful whether any useful comparisons can be made of the action of drugs on bioluminescence *per se* in such widely unrelated animals as those just mentioned, without first assembling detailed information about the action of those drugs on the nervous system and various effectors in each particular form. Adrenaline, for example, is a normal constituent of fish and is produced by suprarenal tissue. Its effectiveness in producing luminescence in *Porichthys* and *Echiostoma* suggests that the nerve fibres supplying the photophores in teleosts are adrenergic, and that the secretion of adrenaline into the blood stream may also be a factor in evoking luminescence. Chromaffin tissue, on the other hand, is rare in polychaetes (Bacq, 1947; Gaskell, 1914). There is now some evidence that cholinergic fibres are widespread in annelids. Acetylcholine brings about muscular contractions in *Arenicola*, *Branchiomma*, *Hirudo* and *Lumbricus*, and eserine augments and prolongs the muscular response to electrical stimulation in some of these animals (Bacq, 1947; Bacq & Coppée, 1937; Katz, 1949; Wu, 1939). Tonic contracture is induced in the isolated extrovert of *Arenicola* by acetylcholine, presumably through excitation of the oesophageal pace-maker (Wells, 1937), and a cholinesterase has been identified in the body wall of *Myxicola* (Bacq, 1937). The positive response of acetylcholine on bioluminescence in *Chaetopterus* fits into this picture, and suggests that cholinergic neurones are involved in the light response.

### *Effects of Various Cations and Unbalanced Salt Solutions*

The effects of various cations on light production were investigated by immersing whole animals in solutions of the several salts. These were all chlorides of Na, K, Ca and Mg. The salts were employed singly and in different combinations to reveal their balancing or antagonistic effects. The solutions, listed below, were used as made up, and also after readjustment of the pH to 8·2 by the addition of NaOH, KOH, HCl, or MgO, as necessary. Variations in pH from 7 to 9 were found not to be a limiting factor in these experiments. Each cation or combination of cations was tried on at least three animals.

1. 0·54M-NaCl 2. 0·54M-KCl
3. 0·36M-$CaCl_2$ 4. 0·36M-$MgCl_2$
5. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol.
6. 0·54M-NaCl, 25 vol. + 0·36M-$CaCl_2$, ½ vol.
7. 0·54M-NaCl, 25 vol. + 0·36M-$MgCl_2$, 2 vol.
8. 0·54M-KCl, 25 vol. + 0·54M-NaCl, ½ vol.
9. 0·54M-KCl, 25 vol. + 0·36M-$CaCl_2$, ½ vol.
10. 0·54M-KCl, 25 vol. + 0·36M-$MgCl_2$, 2 vol.
11. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$CaCl_2$, ½ vol.
12. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$MgCl_2$, 2 vol.
13. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$CaCl_2$, ½ vol. + 0·36M-$MgCl_2$, 2 vol.

Certain cations and combinations of cations had marked stimulatory effects, as the following summaries of the experimental protocols show.

1. *Isotonic* NaCl. Addition of this solution caused luminescence in most or all of the notopodia of the posterior region, followed by weak lighting of the fans in the middle region, and in the aliform notopodia and tentacles.

2. *Isotonic* KCl. This solution immediately caused brilliant and lasting luminescence of all areas: posterior notopodia, dorsal tubercle and fans of the middle region, aliform notopodia and peristomial tentacles. A copious secretion was also discharged from the glands at the bases of the aliform notopodia. This brilliant illumination lasted about 15 min., and then faded away.

3. *Isotonic* $CaCl_2$ had no apparent effect.

4. *Isotonic* $MgCl_2$ had no apparent effect.

5. *Isotonic* NaCl + KCl. This solution produced a bright display almost at once from the notopodia of the posterior region, the dorsal tubercle, and the aliform notopodia.

6. *Isotonic* NaCl + $CaCl_2$. In two specimens a few faint pin-points of light appeared momentarily on some notopodia of the posterior region. Two other specimens were negative.

7. *Isotonic* NaCl + $MgCl_2$. This solution caused luminescence of posterior notopodia, fans, dorsal tubercle, aliform notopodia, and the glands at the bases of the aliform notopodia. The light appeared after about 2 min., was usually brief and rather faint, and affected different specimens in varying degree.

8. 9, 10. *Isotonic* KCl + *either* NaCl, *or* $CaCl_2$, *or* $MgCl_2$. Each of these solutions caused a bright and lasting glow from all luminescent areas, and a copious amount of luminescent secretion from the glandular areas at the bases of the aliform notopodia.

11. *Isotonic* NaCl + KCl + $CaCl_2$. Addition of this solution produced a few faint points of light in the posterior notopodia of one specimen, but had no effect on three others.

12. *Isotonic* NaCl + KCl + $MgCl_2$. This solution caused some notopodia in the posterior region of five specimens to glow brightly, and in two animals evoked brief bright flashes in the alar notopodia, and a brief glow from the dorsal tubercle and glands at the bases of the aliform notopodia as well.

13. *Isotonic* NaCl + KCl + $CaCl_2$ + $MgCl_2$. This solution had no visible effect.

The stimulatory effect of both sodium and potassium on nerve and muscle is well known, and has been reviewed, among others, by Heilbrunn (1943). Sodium stimulates the cardiac ganglion of *Limulus*, and renews rhythmic pulsations in Scyphomedusae on removal of the marginal sense-organs. Potassium stimulates the marginal sense-organs of Scyphomedusae, excites the isolated extrovert of *Arenicola*, and generally stimulates nerve cells and nerve fibres. Magnesium usually exerts a depressive effect and is a general anaesthetic for invertebrates, and calcium, in small amounts, offsets the toxic properties of sodium and potassium (Brown & MacIntosh, 1939; Hodgkin & Huxley, 1945; Rosenblueth, 1950; Wells & Ledingham, 1942).

Studies dealing with the effects of ions on the luminescent response of Metazoa have been confined, hitherto, to coelenterates and ctenophores. There is general agreement that in Scyphomedusae and in ctenophores potassium and calcium evoke and augment luminescence, which fails when these ions are omitted. Sodium, by itself, has little effect. Magnesium reduces luminescence, but when this ion is absent the ability to luminesce is increased (Hykes, 1928; Heymans & Moore, 1924, 1925; Moore, 1926). In general, potassium and calcium are stimulatory in these animals, and the effect is offset by magnesium. These results are somewhat divergent from those obtained with *Chaetopterus*. In this animal potassium has the greatest stimulatory effect, evoking bright luminescence of all regions, and it is seconded by sodium. By itself calcium evokes no luminescence and it fails to suppress the luminescence evoked by potassium. The addition of calcium to a solution of potassium and sodium, however, results in a more balanced physiological solution that fails to stimulate. Magnesium also reduces the stimulatory powers of sodium and potassium. These effects are referred to stimulation of the nerve cells and nerve fibres supplying the luminescent gland cells by sodium and potassium, rather than to any action of these ions directly on the glandular cells. Even after a period of maximal glow evoked by the application of KCl it is still possible to produce the release of further luminescent secretion by direct mechanical stimulation of the photogenic cells in the aliform notopodia. This shows that the glandular cells are still intact and contain a considerable residual amount of photogenic material. Calcium and magnesium, in turn, oppose the stimulatory action of potassium and sodium on the nervous elements.

### *Effects of Hypotonic and Hypertonic Solutions*

Many of the older accounts dealing with bioluminescence refer to the stimulatory effect of fresh water in evoking a luminous response. Panceri (1872, 1878), for example, in studies dealing with the luminescence of marine animals, consistently made use of fresh water to bring about the production of light. This earlier work has been followed up by investigating the effects of various hypotonic and hypertonic solutions of sea water on light production in *Chaetopterus*. To test the effect of a solution, an animal was placed in a dish, dorsal side uppermost, and all sea water was drained off; the solution in question was then added to the dish in sufficient quantity to submerge the animal. The effect of each solution was tested on four or more animals.

### *Hypotonic Solutions*

(1) Distilled water evoked luminescence in about 1 min. Light appeared at first towards the posterior end of the worm, and spread anteriorly to involve the fans, dorsal tubercle, and aliform notopodia.

(2) 20, 30, 40 % sea water. All these solutions caused luminescence in about 1 min. The posterior notopodia lighted first, and the effect gradually spread orally to involve more anterior luminescent regions (fans, dorsal tubercle, aliform notopodia), in varying degree, depending on the animal.

(3) 50 % sea water. This solution evoked luminescence in the posterior notopodia of two out of four animals examined.

(4) 60 % sea water. Three animals gave no response. In a fourth animal there were a few weak flashes from notopodia of the posterior region and from the aliform notopodia after about 1 min.

(5) 70 and 90 % solutions of sea water were without effect.

### *Hypertonic Solutions*

Hypertonic sea water, at strength 150 %, was tried on six specimens. The concentrated sea water was prepared by boiling, and the pH was returned to 8·2 with sodium bicarbonate. It failed to induce luminescence.

These experiments reveal that diluted sea water first evokes luminescence at a strength of about 60 %. The effect increases with greater dilutions, and reaches a maximum in distilled water. Hypertonic sea water (150 %) has no effect.

The mode of action of hypotonic solutions is not clear. They may excite luminescence by a direct osmotic effect, causing cytolysis of the glandular cells; or they may act by differential leaching of ions from nervous elements, giving rise to nervous excitation. *Chaetopterus* is not an estuarine form, and would not be expected to possess any power of osmotic regulation. A tendency is noted for the posterior notopodia to lighten first in hypotonic solution, showing that the profuse mucous secretion of the anterior and middle regions exerts some protective effect.

## Discussion and Conclusions

The present investigation demonstrates that luminescence in *Chaetopterus* is under nervous control. Under localized tactile stimulation light appears only in a restricted area, and even severe injury, amounting to mutilation, fails to evoke widespread luminescence.

Information about the transmission processes involved in the luminous responses is revealed by electrical stimulation of the animal. It is found that low frequencies give a very localized response, confined to a segment or a few segments stimulated, but as the frequency is raised, excitation is transmitted to other regions, until finally the whole animal may lighten. It is concluded that the spread of excitation is a process depending upon the existence of internuncial facilitation in the nerve cord. Through pathways for the luminescent response appear to be lacking, and transmission through the central nervous system involves the build up of an excitatory state at synapses with the arrival of successive stimuli.

The results obtained by electrical stimulation suggest certain ways in which the luminescent response can be regulated. The latter is in some way dependent on the degree of peripheral stimulation. Increased tactile stimulation, presumably, will evoke a higher frequency of discharge, and maintained stimulation a prolonged volley in sensory pathways. At least two factors are operating on the efferent side which determine the magnitude of the response, namely number of neuro-effector units brought into activity and number of nervous impulses discharged. Increase in either the number of efferent stimuli or the number of gland cells excited will result in more light. The significance of the high frequency effect on central nervous transmission in the normal functioning of the animal is more doubtful, but it may represent a mechanism whereby prolonged and vigorous tactile stimulation will bring glandular cells of more distant regions into activity.

There are few comparable studies on other species for comparison. The interesting physiological investigations on nervous control of luminescence in coelenterates and ctenophores show features peculiar to those groups, and necessitate interpretation in terms of the nerve-net existing in those forms. Fujiwara (1935) has shown in *Mesochaetopterus* that electrical stimulation causes the transmission of an excitatory process along the body, resulting in luminescence. Thus, there are certain physiological features common to two genera of chaetopterids, *Chaetopterus* and *Mesochaetopterus*. Other patterns of nervous control in polychaetes are suggested from studies of luminescence in polynoids. Thus in *Acholoë* it has been found that light tactile stimulation gives rise to a local luminescent response, but strong stimulation evokes more widespread luminescence. Transection of the animal causes the posterior fragment to luminesce, but not the anterior piece (Kutschera, 1909). One explanation advanced is that the excitation can only be transmitted caudally, but the reason for this restriction is not clear, and further physiological studies on polynoids and other luminescent forms would be of great interest.

I should like to express my thanks to Dr W. R. G. Atkins, F.R.S., for some helpful criticisms about several aspects of the work, and for the loan of a camera and galvanometer. It is a pleasure to acknowledge technical assistance from Mr F. J. Warren. Part of the expenses incurred in this research was defrayed by a grant from the Government Grant Committee of the Royal Society.

## SUMMARY

The nervous control of luminescence in *Chaetopterus variopedatus* was investigated by various direct and indirect means. Quantitative measurements of the light produced by the animal were obtained by the use of a multiplier photocell and sensitive galvanometer or oscilloscope.

Tactile or mechanical stimulation gives a rather localized luminescent response. The most effective stimuli for evoking luminescence of the conspicuous light glands of the aliform notopodia are tension and pressure acting on segment XII.

Electrical stimulation of segment XII (condenser discharges) causes the appearance of light in the glands on the aliform notopodia. The mean latent period, as determined from oscilloscope records, was 4·2 sec., and the time taken to reach maximal intensity from first deflexion was 10·3 sec.

A single shock causes the appearance of light, and the intensity of the response is increased by increasing the voltage or the number of stimuli. Raising the voltage throws more efferent neurones into activity. Augmenting the number of stimuli results in an enhanced effect, and more luminescent material is secreted.

The preparation fatigues readily, and successive periods of stimulation give greatly decreased responses. No recovery was observed under experimental conditions after a rest period of 3 hr.

At low frequencies of stimulation the response is restricted to the segment or few segments directly stimulated. Raising the frequency brings more segments into luminescence. This effect is ascribed to some process of internuncial facilitation in the nerve cord.

The effects of four autonomic drugs were tried. Adrenaline had no effect. Acetylcholine and nicotine were weakly excitatory. Acetylcholine produced luminescence in fragments lacking central nervous tissue as well as in pieces containing nerve cord; it has an excitatory effect, therefore, on peripheral elements. There was no noticeable augmentatory effect with eserine. The evidence suggests a nicotine-like action of acetylcholine acting peripherally.

Isotonic solutions of NaCl, KCl, $CaCl_2$ and $MgCl_2$ were tried on the preparation. K and Na were excitatory, particularly the former. Addition of Mg reduced the excitatory effect of K and Na, and Ca inhibited the luminescence usually evoked by K and Na salts. A balanced salt solution, containing K, Na, Ca, and Mg, in the proportions in which they occur in sea water, failed to produce luminescence. The excitatory effects of K and Na, and the opposing effects of Ca and Mg, are ascribed to stimulation of nervous elements concerned with luminescence.

Hypotonic solutions and fresh water are stimulatory, luminescence appearing in about 60% sea water. The effect is not clear; it may act through cytolysis of glandular cells, or by differential leaching of ions.

Hypertonic solutions (150% sea water) have no excitatory effect.

A review of the literature dealing with luminescence in *Chaetopterus* is given, and the physiological results obtained in the present investigation are compared with observations on several other forms.

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# PROCESSES OF ENRICHMENT OF SURFACE WATER WITH NUTRIENTS DUE TO STRONG WINDS BLOWING ON TO A CONTINENTAL SLOPE

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(Text-figs. 1–4)

Biological and physical evidence suggests that the area south-west of Ireland is one of loss from the Celtic Sea. In winter the shelf water there may cascade to 400 m. or even deeper (Cooper & Vaux, 1949). All the evidence suggests that new water enters the Celtic Sea and English Channel over the continental slope between Ushant and the Sole submarine promontory 250 miles to the west. No evidence exists that the Atlantic surface waters are ever rich enough to account for the enrichment of the English Channel observed in the nineteen-twenties. Although the existence then of sufficiently rich oceanic surface water cannot be excluded, it is much more probable that the enrichment was brought about by some form of upwelling. The cause of this is thought to be composite. Only a few times in a century may the component phenomena work together to produce the maximum effect. Each component needs separate study.

There may be two distinct effects of a strong wind blowing on to the continental slope from the south. Such a wind will force light nutrient-poor water against the slope (assumed to extend to the surface of the sea) to form a cushion of considerable depth above sloping isosteres—surfaces of equal density—stable only while the wind lasts (Sandström, 1918; reproduced by Harvey, 1928, fig. 25A). Potential energy has become stored in the water. As soon as the wind dies down and the stress is removed from the sea surface, the potential energy is converted to kinetic energy. Each isosteric surface would then oscillate about its mean level. If there were no frictional losses, this oscillation would go on for ever.

The conditions against an actual continental slope are rather different, since it is usually bordered by a continental shelf. There, when the heavy deeper water rises against the slope, it would spill over the edge on to the continental shelf. Some mixing and enrichment with nutrients of continental shelf water would occur, but the effect is unlikely to be great and it would be important only locally.

But in a submarine valley, such as that at 48° 13′ N., 9° 21′ W., which becomes narrower and shallower as it cuts back into the shelf, such spillage water would become canalized. Conditions would come to resemble those which create a tidal bore or eagre in the Rivers Severn and Trent. It would seem probable that such a constricted core or eagre of deep water could be projected for many miles on to the continental shelf whence it would return only slowly on the next downward swing of the boundary layer over deep water. This mechanism would be especially favoured if a submarine valley in the slope heads into one of the shallow troughs which dissect the south-western Celtic Sea. Indeed it would provide a means for preventing such troughs from silting up.

The inference is that areas of the sea lying immediately shorewards of a submarine valley should be especially favourable for outbursts of phytoplankton not only in spring but in summer as well. Submarine eagres of this kind may well often occur but seem insufficient to account for much enrichment of large areas such as the Celtic Sea.

Except when cascading is occurring (Cooper & Vaux, 1949), waters near the headings of submarine valleys should become richer in total phosphorus and other 'total' nutrients than those lying near to an undissected continental slope.

Sandström (1918, p. 234) further developed this idea into his concept of 'jibing' of water masses in a high wind. When the external forces, such as wind stress, acting on the sea water reach a magnitude exceeding the highest possible value which can be sustained by the Archimedean forces, a catastrophe takes place and an entirely new state of affairs is brought about, exactly as when the limit of elasticity of a solid is exceeded.

The maximal value of the Archimedean forces is reached when the isosteres become vertical. Should the external forces exceed that required to produce vertical isosteres, then the surface waters will *capsize*, as exemplified in detail in Fig. 1. Then, light water is brought down beneath heavier, the stability is upset and a strong vertical convection ensues whereby the *whole of the water affected is mixed up into one single homogeneous layer*. The specific volume of this layer will be equal to the mean specific volume of the strata of which it is composed, and between this and the water beneath there will be a sharply defined difference of density. In the homogeneous layer there will be no isosteres and, consequently, no Archimedean forces will arise, so that the water therein contained will follow without resistance the direction of any external force acting upon it. The circulation will be highly intensive so that the water will continue homogeneous, and exert a continual friction upon the layer beneath, thus maintaining the sharply defined limit of density between the two. This friction occasions a gradual absorption of the water from the lower layer, so that the upper one will tend to increase in volume, density and nutrient content.

Sandström gave to this process the name 'to jibe'. 'Jibe' is a variant of 'gibe' and means 'to taunt'; either 'gybe' or 'jib' may have been intended.

Their meaning is to swing from one side of a mast to the other. 'Jib' has other meanings; applied to a horse it signifies to stop suddenly, to move restively sideways and backwards. The term 'to jib' could be used but is not particularly appropriate for the present purpose. 'Capsize' is more fitting.[1]

In Fig. 1, panels C and D, as applied to the Celtic Sea, part of the energy of the wind will be expended on raising the level of the water over the continental shelf (i.e. in the Celtic Sea), part in forcing water through escape channels, such as the Straits of Dover and the North Channel, and part in initiating a cyclonic circulation of water to escape south-west of Ireland.

South-west of Ireland the gales most likely to provoke capsizing of water masses will be from the south-west and west, and these are the prevailing winds and those which most often reach gale force. They are commonest in winter and will then combine with cascading and resonance phenomena in the 'South Porcupine submarine indentation' to produce vertical mixing to a very considerable depth (cf. Fig. 2). The waters most concerned will be either oceanic surface waters or water recently cascaded from the continental shelf. There is in this area only rarely a mechanism for enriching the continental shelf with deep nutrients on any considerable scale. Even when enrichment occurs here, the dominant cyclonic circulation will tend to carry the surface water away from the Celtic Sea. The waters over the Porcupine Bank might, however, benefit. Whenever cascading plays a part it will tend to reduce enrichment from deep water by any other mechanism.

Along the southern edge of the Celtic Sea, the strong winds most favourable for capsizing would blow from the south-east or south. These winds are less common than the south-westerlies and westerlies. Moreover, in this area, there is much less cascade water so that, if capsizing occurs, it may bring about mixing with the deeper North Atlantic Central water and even with the Mediterranean or Gulf of Gibraltar water at 800–1200 m. depth, both relatively rich in nutrients (Cooper, 1952). All in all, the most favourable conditions for enrichment of the southernmost Celtic Sea by capsizing are likely to occur after the breakdown of the summer thermocline in autumn. Southerly gales in November and December are likely to be more effective in bringing up nutrients than those in February or March. The usual cyclonic circulation of the Celtic Sea will tend to transport such enriched water on to the continental shelf and into the English Channel.

Conditions to initiate capsizing of water masses are likely to occur over continental slopes backed by extensive shallow seas, for there the surface ocean waters are relatively free to press inwards, whereas the root of the water mass will be stopped completely by the continental slope.

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[1] The writer would prefer to introduce the term 'culbute' derived from the French *culbuter* which suggests all that 'capsize' and 'somersault' do, but much destructive power as well. Majority opinion in this laboratory is that addition of yet another word to the technical jargon of science cannot be justified and that 'capsize' will serve (see Addendum, p. 463).

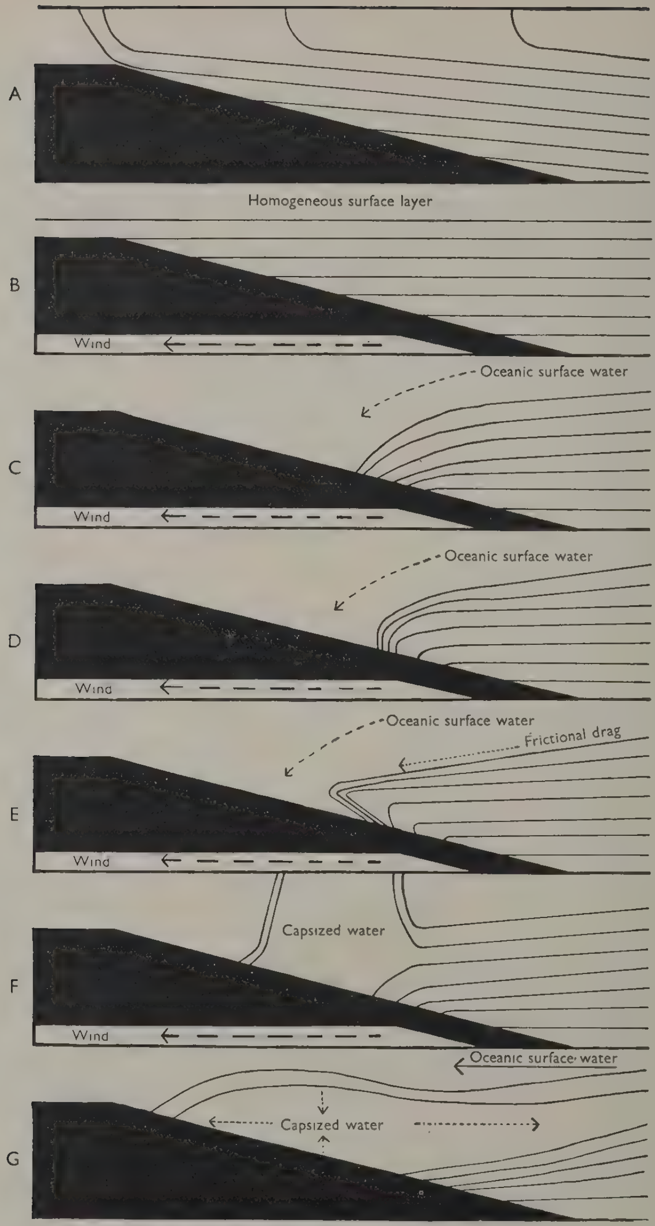
A
Homogeneous surface layer
B
Wind
Oceanic surface water
C
Wind
Oceanic surface water
D
Wind
Oceanic surface water
Frictional drag
E
Wind
Capsized water
F
Wind
Oceanic surface water
Capsized water
G

Fig. 1.

Capsizing is essentially a wave phenomenon and may be compared with the breaking of a roller approaching a beach. By analogy with what happens to a swell approaching an ordinary coastal bay, over a submarine terrain such as that illustrated by Cooper (1952, fig. 10), there should be a tendency for the destructive energy created by capsizing to be concentrated over the submarine spurs and for the headings of the valleys to be relatively quiet. Capsizing as a mechanism for surface enrichment with nutrients is likely to be more effective over strongly dissected sections of the continental slope than over smooth areas.

In September 1950, Dr C. F. Mortimer kindly allowed me to experiment with his model built to illustrate the observed effect on water movements of a strong wind blowing along a stratified lake, Windermere. Mortimer's model, developed quite independently, resembles that illustrated by Sandström (1918, fig. 45), except that it has sloping ends. At the time interest was concentrated on establishing that internal waves from a distant source could produce upwelling phenomena. Although something of the sort could be made to happen, the scale did not seem adequate to account for observations in the ocean.

In these experiments the process of capsizing and the destructive turbulence resulting was demonstrated, yet, I regret to say, it was not until 6 months later, when the theory of capsizing over a continental slope had been further developed from Sandström's work, that the behaviour of the model was understood (see Addendum, p. 462).

A number of phenomena, such as the distribution of mass and of nutrients which would result from currents running parallel to the continental slope

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**Legend to Fig. 1.**

Fig. 1. A, a frequent pattern of isosteres south of the Celtic Sea in winter when the uppermost 75–100 m. of water in the ocean is homogeneous and is overlying water with density and content of nutrient salts increasing downwards. B, a pattern of isosteres in winter over the continental slope, drawn to a scale of 1:4, with no forces operative. The amount of light water which will later lie to windward is considered unlimited. C and D, cushioning of light oceanic surface water against the continental slope brought about by on-slope gales. The resistance of the solid slope to further progress of the foot of the light water is, however, absolute causing the isosteres to curl and ultimately to become vertical. Restoring Archimedean forces in D have then become zero. E, the drag of the surface wind current will draw the upper strata of stratified water with it leading to an unstable density inversion as illustrated. F, the unstable tongue of heavier water will capsize violently, leading to a homogeneous mass of mixed water extending from the surface to the depth of the bottom of the capsizing water mass. New isosteres, bracketing the capsized water mass, are so created. G, the newly formed surface water will be heavier than the surface water inshore and to seaward and will subside to form a lens of homogeneous water at its appropriate density level and will be replaced by fresh oceanic surface water blown in from seaward. Processes D–G must be considered as simultaneous parts of a continuous process, with the line of capsizing receding from the continental slope and the maximum depth of the phenomenon increasing as the gale proceeds. Consequently the water blown on to the continental shelf of the Celtic Sea by a strong southerly gale should be entirely capsized water and richer in nutrients than it would be if it were solely oceanic surface water. Moreover, the nutrient content of the water passing on to the shelf should increase as the gale proceeds, and the depth of capsizing becomes greater.

have been considered as means of enrichment of surface water with nutrients from deeper layers. None, considered singly, seems able to account for the observed occurrence of nutrients. The concept of capsizing of a water mass over the southern continental slope of the Celtic Sea during strong southerly gales is the first to promise a mechanism on a scale great enough to explain the observed results.

No research ship is ever likely to make direct observations of capsizing water masses during strong on-slope gales. Indeed a shipmaster is likely to take steps to get away from an area of capsizing as quickly as possible. By the time the wind had dropped sufficiently to allow of observations, much of the direct evidence would have vanished. Confirmation will need to be sought by indirect means.

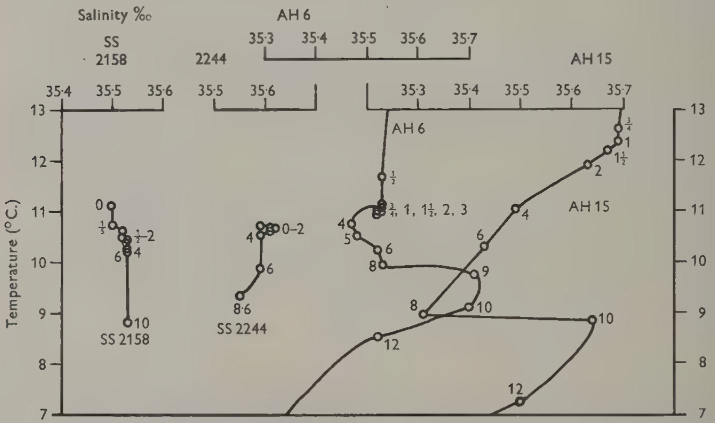

Fig. 2. Temperature-salinity relationships: on two occasions at station SS, 50° 34′ N., 11° 17′ W., on the edge of the 'South Porcupine' submarine bight, south-west of Ireland (SS2158, 14. v. 25, and SS 2244, 19. ii. 27); at *Armauer Hansen* station 1914/6 (5. vi. 14) on the southern edge of the Celtic Sea (cf. Cooper, 1952, figs. 8 and 9); and at *Armauer Hansen* station 15 (9. vi. 14) in the North Atlantic 400 miles from the continental slope. The small figures represent depths in hundreds of metres. The diagram illustrates the vertical compression of properties which may occur in the submarine bight and to a lesser extent anywhere on the continental slope.

A greater understanding of the process of capsizing may contribute to the safety of vessels passing over the continental slope, in particular those engaged in the hake fishery.

Capsizing has to be considered as one only of a number of mechanisms peculiar to the region of the continental slope which contribute in different degrees to the enrichment of the English Channel with nutrients. Atkins's (1923) first measurements on 7 March 1923 showed that the phosphate content of the English Channel at E1 (50° 04′ N., 4° 22′ W.) was then very high

(0·71 μg.-atom/l.). It is of interest that the table of mean wind conditions over the western English Channel (Dietrich & Wyrtki, 1951, used by permission of the Hydrographer of the Navy) shows that in February 1923 the monthly mean wind blew at 8·1 m./sec. from direction true 214°, a monthly mean velocity which has never been exceeded since from any direction. None the less, detailed examination of records shows that it would be too facile to attribute the observed distribution of nutrients in March 1923 solely to capsizing water masses over the continental slope during the preceding south-westerly gales. The event needs to be remembered as one only in the complex of events we are seeking to understand.

Temperature-salinity diagrams for stations 49, 51 and 68 (Cooper, 1952, fig. 4) worked by the *Thor* in 1906 (Schmidt, 1912) are shown in Fig. 3. The middle station 51 is strikingly different from stations 49 and 68, from all others worked by the *Thor* and from International Station E4 (48° 27′ N., 6° 35′ W.) worked 6 days earlier. The isohaline water extended from 50 to 800 m., suggesting that the waters at station 51 had been subjected to more intense vertical mixing. At all the nine deep-water stations worked, except one, marked thermal stratification of the uppermost water layers had become established. The exception was again station 51, where the surface water was only 0·15° C. warmer than at 100 m., the uppermost 50 m. being completely isothermal. The maintenance of such homogeneity in late spring must have demanded powerful forces bringing about vertical mixing.

The position of station no. 51, 48° 07′ N., 9° 03′ W. shown by Cooper (1952, fig. 10), was near a dissected section of the continental slope. Any water movements in such an area should facilitate vertical mixing and capsizing there is likely to be especially strongly developed.

The Daily Weather Reports of the Meteorological Office for November 1905–May 1906 have been examined. The winter was not notably stormy. There were south-westerly gales (Beaufort force 7 or 8) in the area on 22 and 26 November, and a south-south-easterly gale on 18 December. The stormiest period was the first fortnight of January. These were the only gales which could have caused severe capsizing, but they were at the season suspected of being most favourable for nutrient enrichment. The north-westerly gales of 8, 11 and 12 February and 12 March could not have caused capsizing in the southern area. There have been many winters more favourable for capsizing than that of 1905–6.

It has been earlier suggested (Cooper, 1947) that internal waves may play a part in raising nutrient-rich deep water on to the continental shelf. So they may, but now it seems that in this area their influence will be very small compared with that of capsizing. It seems more likely that some internal waves in the ocean may arise from intermittent capsizing over distant continental slopes. This is a process which could be readily established by repeated observations of temperature and salinity at standard depths at a position some hundreds of miles off a continental slope against which a heavy gale was known to be blowing.

The exceptionally powerful vertical thrusts visualized as occurring beneath a capsizing water mass, followed by subsiding of the relatively heavy new surface water and recovery of the deeper water of the same density into a thinner but more extensive lenticular water mass at mid-depths, is a process which must necessarily initiate wave motion in the lower boundary of the

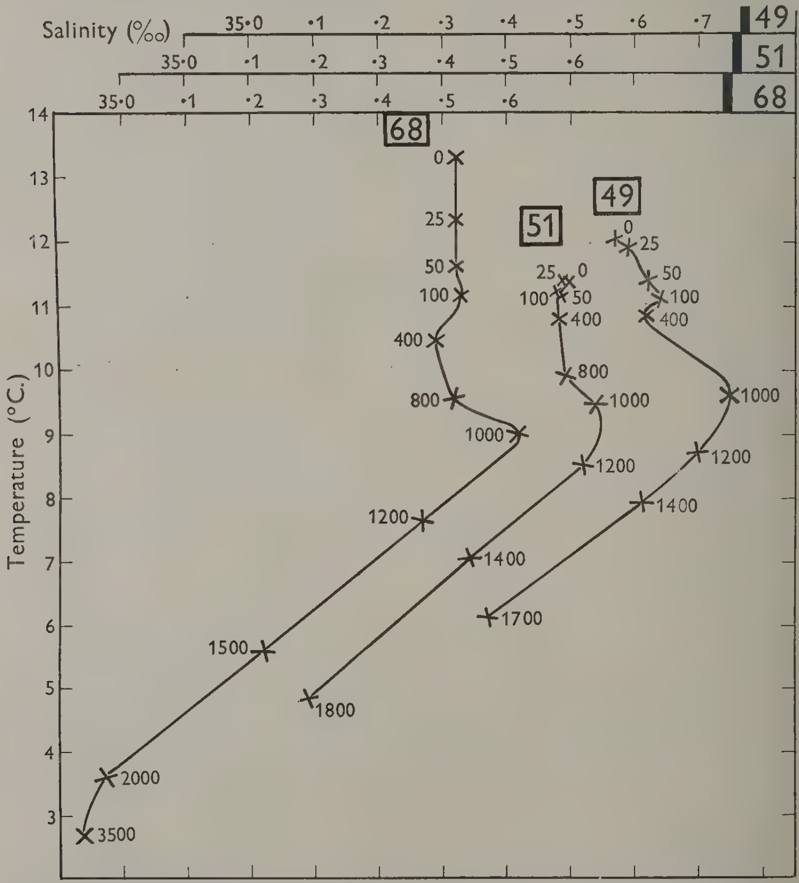

Fig. 3. Temperature-salinity diagrams for three stations (49, 51, 68) worked by *Thor* in May 1906 (see Cooper, 1952, fig. 4). The numbers refer to depths in metres.

homogeneous water. Internal waves may be a result, not a cause, of a process that leads to enrichment with nutrients of surface waters.

A stratified or laminated water mass underlying a quiescent one, already homogenized by capsizing, may be compared with the leaf-spring of a railway wagon or motor car at rest. In the open ocean, the vertical thrust due to subsequent capsizing of a water mass—if indeed such ever occurs there—would be taken up by the laminated water mass as by a leaf-spring and the energy smoothly dissipated as internal waves. There is no reason to suspect that much dissipation of energy would occur due to friction or turbulence. But against a continental slope, and especially against a strongly dissected one, this 'leaf-spring' of laminated water masses would grind forcibly, so that much of the energy of the vertical thrust due to overhead capsizing would be dissipated by turbulent mixing.

The detailed examination of the Irish records at station SS (Cooper, 1952) has shown that much vertical mixing occurs between 600 and 1000 m. Two of the most extreme occurrences are presented in Fig. 2. On occasion cascading from the north would provide a partial explanation of the observed distribution of properties, but it is clear that it cannot always do so. On some occasions the distribution of temperature has been such as to make it highly improbable that any considerable proportion of the surface water immediately overhead had been carried down. The phenomenon is one of mixing, confined to the deeper strata, without complete homogenization.

It is inconceivable that this phenomenon arises from the mixing action of surface waves. Much thought has been given to internal waves as a cause of such deep turbulence, but no records exist of internal waves in the ocean of sufficient magnitude to produce the observed distribution of properties against the slope.

'Leaf-spring' dissipation of energy beneath a capsizing water mass against a dissected continental slope promises a mechanism able to transmit to very considerable depths energy imparted to the sea surface, and of sufficient magnitude to produce the observed distribution of properties between 600 and 1,000 m.

This process of capsizing, if it can be firmly established, would influence the biological cycle in the sea in many very varied ways. The hypothesis fits qualitatively with such local observations as have been examined. It is not proven, and is presented solely as a basis for further quantitative work.

## SUMMARY

Some physical processes are examined which may cause enrichment of the surface layers of the sea from deep reserves of nutrients.

Winds blowing intermittently towards a continental slope may produce vertical oscillations which bring about spillage of deeper nutrient-richer water from the ocean on to the continental shelf. Submarine valleys cut in the continental slope should canalize such spillage water into narrow streams.

Sandström's concept of capsizing of water masses in a high wind has been further developed for the conditions existing over a continental slope. Capsizing of water masses is more likely to enrich the surface layers over the southern rather than over the western continental slope of the Celtic Sea. Capsizing is likely to be especially intense over submarine spurs projecting from dissected regions of the continental slope.

Data collected by the Danish research ship *Thor* in 1906 is adduced as evidence for capsizing over a dissected slope.

Internal waves in the open ocean may possibly be created by the vertical thrusting of capsizing water masses over a continental slope.

The deeper stratified water underlying a region of capsizing has been compared with a leaf-spring of a vehicle. Dissipation of the energy of capsizing in such a leaf-spring of stratified water would produce a distribution of properties such as that often reported from the Irish investigations.

## ADDENDUM (ADDED IN PROOF)

Photographs to illustrate the process of capsizing have been obtained at the Windermere Laboratory of the Freshwater Biological Association in Dr C. H. Mortimer's (1951) experimental tank. In this the surface layer of water may be warmed and made lighter by two hot wires stretched the length of the tank, and then labelled by means of a dye. Electric blowers simulate wind blowing over a stratified lake or sea.

In the ocean the theory of capsizing of water masses over a continental slope requires a very large reservoir of light surface water lying in the ocean to windward and opportunity for some surface water to be driven on to the continental shelf to leeward. In our area the Celtic Sea and its neighbouring channels provide such opportunity. These conditions the tank cannot provide. Although capsizing has been observed on the 'lee slope' of the tank, it has not been possible to photograph it.

When the blowers are stopped the light surface water in the tank swings from the leeward to the windward end of the tank where a process closely akin to but not identical with capsizing occurs. This is illustrated in Fig. 4. The uncoloured water is heavier than the coloured water and, in the ocean, the condition illustrated should be quickly followed by cataclysmic mixing. Though there is an element of fake in these pictures, none the less they should assist the reader to visualize the process of capsizing which has been described.

The writer is indebted to Mr H. C. Gilson, Director, for placing the facilities of the Windermere Laboratory at his disposal, to Dr Mortimer for the use of the tank and to him and Mr E. Ramsbottom for experimental and photographic assistance.

The term 'capsizing' (see p. 455, footnote) has been discussed with hydrographers during the meeting of the International Council for the Exploration of the Sea at Amsterdam in October 1951. It was clear that to some people the word conjured up a picture of a complete turning-turtle without very much mixing. The most essential part of the process is cataclysmic mixing; overturning is also essential, but in any one incident it need not be complete.

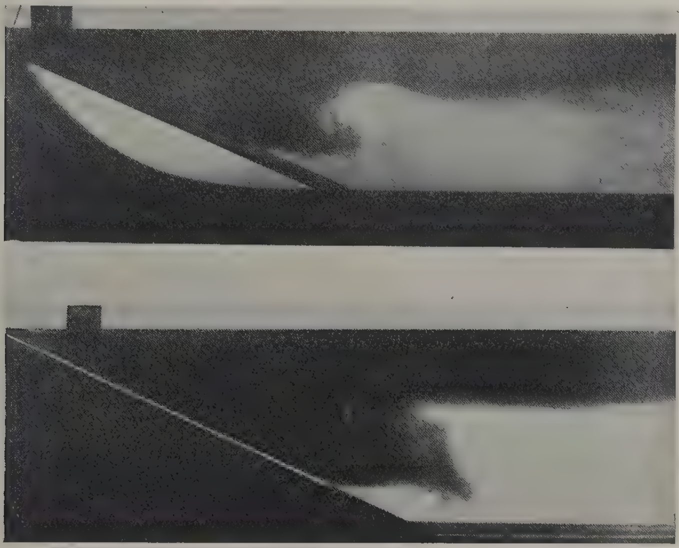

Fig. 4. Two photographs in a model tank to illustrate the process of capsizing of water masses over a continental slope. In both pictures the continental slope is represented by a sheet of metal; in the lower one the dead water beneath the plate has been masked and the boundary between the capsized water and the 'continental slope' has been lightly touched up.

The French word *culbuter*, meaning 'to upset violently resulting in a confused heap or jumble', expresses much better than any English word what is in mind. Mr G. A. Steven, who suggested the apt word 'cascade' for another kind of event over the continental slope, feels strongly that 'culbute' is much the more descriptive word and that its introduction into oceanography is justified. Oceanographers, if they find the need to use the hypothesis, are left to choose the term they think most fitting. If accepted for use in English speech the pronunciation of 'culbuṭe' would be better anglicized.

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# THE PHYSICAL AND CHEMICAL OCEANOGRAPHY OF THE WATERS BATHING THE CONTINENTAL SLOPE OF THE CELTIC SEA

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(Text-figs. 1–15)

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Knowledge of the hydrography of the English Channel and Celtic Sea is needed as a background for the life histories of the mackerel, pilchard and herring and, indeed, of every organism living within range of the Plymouth Laboratory. Such knowledge can never be fully attained until we know more of the exchanges with the deep Atlantic Ocean which take place 200–300 miles to the south-west and west over the continental slope. Moreover, at the slope we shall need to know not only what waters move in and out but what move up and down. Long ago Storrow (1925), and no doubt others, saw clearly some of the problems here to be discussed, but they were unable to bring factual evidence to bear. A critical reconstruction of the considerable but fragmentary observations in the neighbourhood of the continental slope of the Celtic Sea will be presented here and supplemented by observations made in 1950 with the generous co-operation of the vessels of the National Institute of Oceanography (Discovery Committee) and in 1948 by H.M. Surveying Ship *Dalrymple*. Though many of the conclusions remain tentative, it should now be easier to design observational work at sea to test specific hypotheses at the right time and place by the methods of experimental oceanography. The numerical results in 1950 will be published by the Conseil International pour l'Exploration de la Mer.

In addition to acknowledgements in the text and to many colleagues at the Plymouth Laboratory, thanks are due to the Hydrographer of the Navy for his cordial assistance in many ways and to Dr J. N. Carruthers of the Hydrographic Office, who has frequently constructively assisted from his unrivalled knowledge of the literature. He and Mr G. A. Steven of this laboratory have provided anvils upon which some of the ideas and nomenclature have been hammered out. Mr F. A. J. Armstrong, not only by carrying out all the laboratory analyses and by his critical faculty but by relieving me of many day to day duties, has much furthered this work. Insufficient acknowledgement has been made in the text of the great debt due to the writings of the Scandinavian school of oceanographers, in particular those of B. Helland-Hansen, F. Nansen, J. W. Sandström and H. U. Sverdrup and to those of the Canadian investigator, A. G. Huntsman, and the American, C. G. Rossby.

## The Mediterranean or Gulf of Gibraltar Water

The highly saline deeper water (salinity > 38‰) from the Mediterranean Sea spills over the sill of the Straits of Gibraltar and flows downhill, mixing vigorously the while with Atlantic water mostly North Atlantic Central water (p. 479) with a salinity around 36‰. The mixed water attains a density around $\sigma_t$ 27·6–27·8 and spreads out as an intrusive plate or tongue into the Atlantic at around 1000 m. depth, slowly mixing further with the waters above and below (Helland-Hansen & Nansen, 1927). This 'Mediterranean' water has never been shown to be of importance for studies of surface hydrography in our area, but there is little doubt that it is.

When only salinity, temperature and oxygen have been considered the name 'Mediterranean' has been clear and unambiguous but, when applied in nutrient and productivity studies, it is misleading. 'Mediterranean' suggests a water very poor in nutrients. In fact the 1000 m. stratum here is relatively rich, since it includes a large component of enriched Intermediate or Central water from the equatorial Atlantic at 700–1200 m. depth. When this water upwells here, the upper layers will not be seriously impoverished, as the name 'Mediterranean' would suggest, but enriched. A truly descriptive name should suggest that we have to do with a new water mass created in the Atlantic Ocean west of the Straits of Gibraltar which Vallaux (1936) has neatly described as the 'Gulf of Gibraltar'. In this paper, henceforth, the term 'Mediterranean water' will be replaced by 'Gulf of Gibraltar water'. I am indebted to Dr J. N. Carruthers for suggesting this.

From the way in which this water has been formed one would expect it to be markedly heterogeneous (Nielsen, 1912, pp. 179–82), and in our area it is. It cannot be identified by any point on a temperature-salinity diagram but only by an area. The point $G$ (9·00° C., 35·70‰ $S$) which we shall use to represent it on $T$–$S$ diagrams is a useful statistical fiction which expresses the fact that, during the slow mixing of Gulf of Gibraltar water with North Atlantic deep water (and no doubt with North Atlantic Central and cascade waters), short-period and considerable fluctuations in the properties of the former become ironed out so that the mixed water approximates closely to the linear temperature-salinity relation:

$$S = 35{\cdot}25_8 + 0{\cdot}14_7(T-6). \qquad (1)$$

Before the results of the 1938 International Gulf Stream Expeditions had reached this country (see p. 486) this expression had been derived by the method of least squares from *Armauer Hansen* stations 7–15 of 1914 (Helland-Hansen & Nansen, 1927), and other scattered observations where oxygen observations were available.

Although the temperature and salinity of the Gulf of Gibraltar water vary much, the percentage saturation with oxygen does not. Between *Armauer Hansen* stations 7 and 15 (Gaarder, 1927) the temperature of this water ranged from 8·37 to 10·44° C. and the salinity from 35·52 to 35·75‰, whereas the oxygen content lay always between 65 and $68{\cdot}_5$% saturated. This property will sharply distinguish Gulf of Gibraltar water from cascaded or 'capsized' water (Cooper, 1952*a*) of similar temperature and salinity, but not from North Atlantic Central water which at similar depths has similar oxygen percentage saturation.

The impoverished deeper water of the Mediterranean is even more deficient in phosphate than it is in nitrate; it has a large positive anomaly of the nitrate-phosphate ratio. In the Gulf of Gibraltar this Mediterranean water mixes with North Atlantic Central having (for the North Atlantic) a high content of nutrients and a normal nitrate-N–phosphate-P ratio of about 15:1. Off the Iberian Peninsula, Thomsen's (1931) results showed that the nitrate-phosphate ratio in the newly formed Gulf of Gibraltar water, after correction for phosphate salt error, may be as high as 40:1. By the time it has flowed to the border of the Celtic Sea, this water may be still poorer than North Atlantic Central water at the same depth but, from the point of view of upwelling, it must be regarded as a relatively rich water, in which the anomalous nitrate-phosphate ratio has almost disappeared (Cooper, 1937, 1938*a*).

The very variable extension from time to time of Gulf of Gibraltar water was shown by five stations worked by the present H.M.S. *Challenger* at a single truly oceanic position 44° 36′ N., 20° 00′ W. (Cons. Int., *Bull. Hydrogr.*

for the respective years), supplemented by the nearby *Deutschland* station (Reihe) 4 (Brennecke, 1921) (Table I).

For standard depths on the six occasions mean values of temperature and salinity have been calculated; the deviations from these means are presented in Fig. 1, from which it will be seen that between 0 and 700 m. depth the range of temperature and salinity was 1·2° C. and 0·20‰ respectively. The relatively much larger fluctuations at 750 and 1000 m. depth are more clearly shown by the standard deviations at standard depths graphed in Fig 2. Most striking of all was the very rapid increase in both temperature and salinity in the 4½ months between 29 November 1932 and 14 April 1933 (Fig. 3 and Table II). Thus at the level of the Gulf of Gibraltar water there were large variations from year to year in the middle of April and very rapid changes in the course of a few months. This conclusion is confirmed by the findings at the Irish station SS on the continental slope (Table XV and Fig. 2), and would probably have been found anywhere in the eastern North Atlantic.

TABLE I

| Ship | Station no. | Date | Lat. | Long. | Depth (m.) |
|---|---|---|---|---|---|
| *Deutschland* | 4 | 20. v. 11 | 45° 13′ N. | 20° 07′ W. | — |
| *Challenger* | 1292 | 29. ix. 32 | 44° 37′ N. | 20° 00′ W. | 4372 |
| *Challenger* | 1318 | 14. iv. 33 | 44° 35′ N. | 19° 56′ W. | 4170 |
| *Challenger* | 1556 | 18. iv. 34 | 44° 35′ N. | 20° 00′ W. | 4315 |
| *Challenger* | 1666 | 14. iv. 35 | 44° 40′ N. | 20° 00′ W. | 4546 |
| *Challenger* | 1772 | 13. iv. 36 | 44° 36′ N. | 20° 00′ W. | 4546 |

TABLE II

| Depth (m.) | Temperature (° C.) | | | Salinity (‰) | | |
|---|---|---|---|---|---|---|
| | 29. ix. 32 | 14. iv. 33 | $\Delta T$ | 29. ix. 32 | 14. iv. 33 | $\Delta S$ |
| 750 | 8·84 | 9·76 | 0·92 | 35·37 | 35·56 | 0·19 |
| 1000 | 7·26 | 7·86 | 0·60 | 35·35 | 35·76 | 0·41 |

The capacity of these deep-water movements to transport heat about the world is great. Thus this short-period increase in heat content at 44° 36′ N., 20° 00′ W. of a column of water 1 cm.$^2$ cross-section would have been sufficient to raise the temperature of all the air above a surface of 308 cm.$^2$ by 1° C. Otherwise stated, the increase in temperature of the water below 100 square sea miles would have been sufficient to raise the temperature of all the air over Great Britain by 0·5° C. The Gulf of Gibraltar water should not be regarded as permanently sealed down and of no account in surface oceanography and meteorology.

Vallaux (1936) has already directed attention to the highly heterogeneous nature of the Gulf of Gibraltar water. He pictures it as fragmented into a series of globular masses dispersing both in depth and expanse through the North Atlantic and gradually merging with it.

In 1906 the *Thor* (Schmidt, 1912), in the course of her investigations on the breeding place of the eel, worked a number of hydrographical stations along

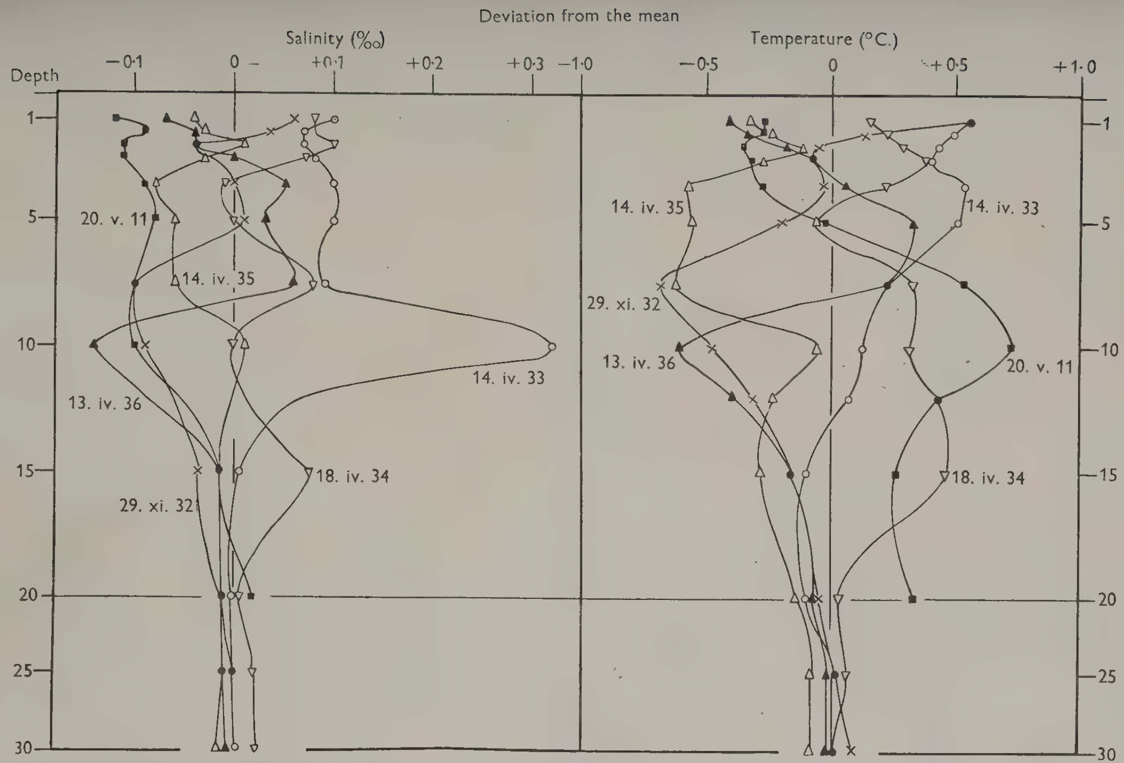

Fig. 1. Salinities (left) and temperatures (right) from standard depths at six stations in the North Atlantic near 44° 36′ N., 20° 00′ W. (Table I), expressed as deviations from the respective mean values at each depth. Black circles indicate coincident points on two or more curves. Depths in hundreds of metres.

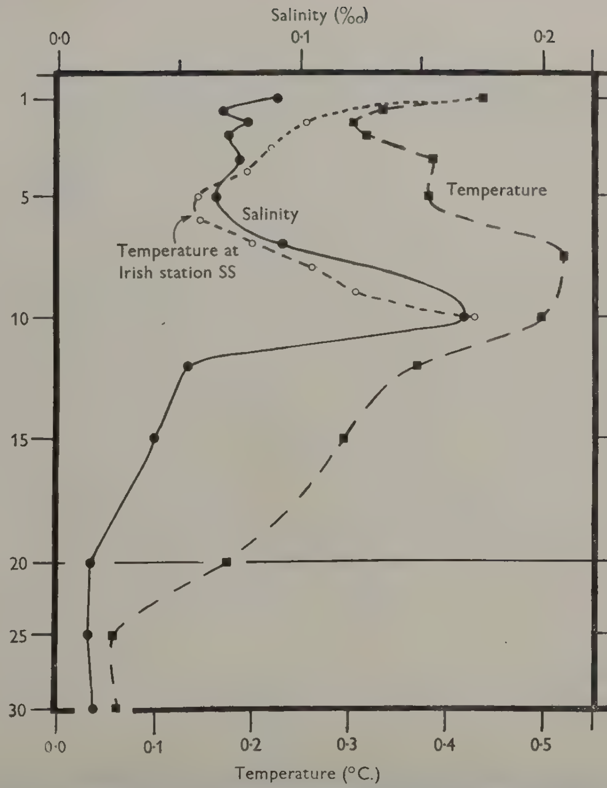

Fig. 2. Standard deviations of temperature and salinity based on six sets of observations at or near 44° 36′ N., 20° 00′ W.; also (open circles) standard deviations of temperature from twenty-nine sets of observations at the Irish station SS (50° 34′ N., 11° 17′ W.) from Table XV. Depths in hundreds of metres.

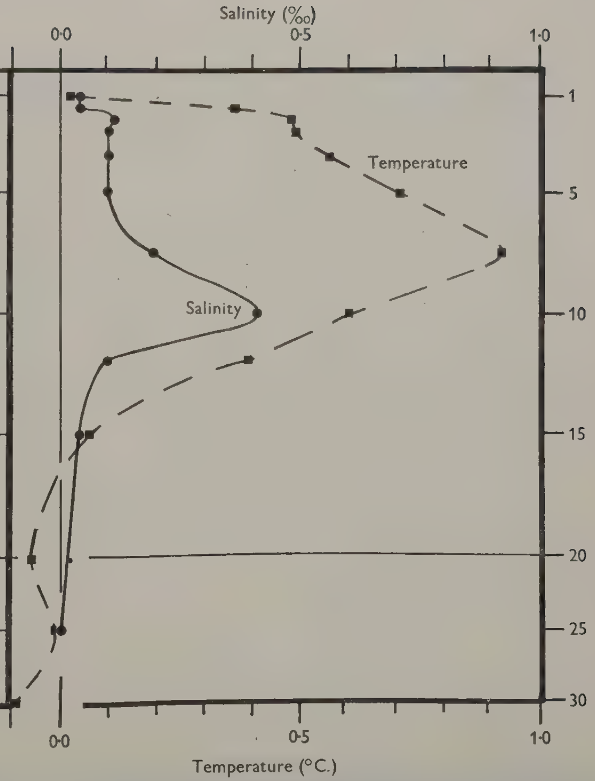

Fig. 3. Increase in temperature and salinity between 29 November 1932 and 14 April 1933 at 44° 36′ N., 19° 58′ W. Depths in hundreds of metres.

the slope of the Celtic Sea and Bay of Biscay. On Fig. 4 some stations worked between 10 May and 17 June are denoted by circles and some between 26 August and 3 September by crosses. Section I (Fig. 5) ran in deep water along the edge of the slope. It is clear that the wedge of highly saline Gulf of Gibraltar water was held into the right on the Franco-Iberian coast, and

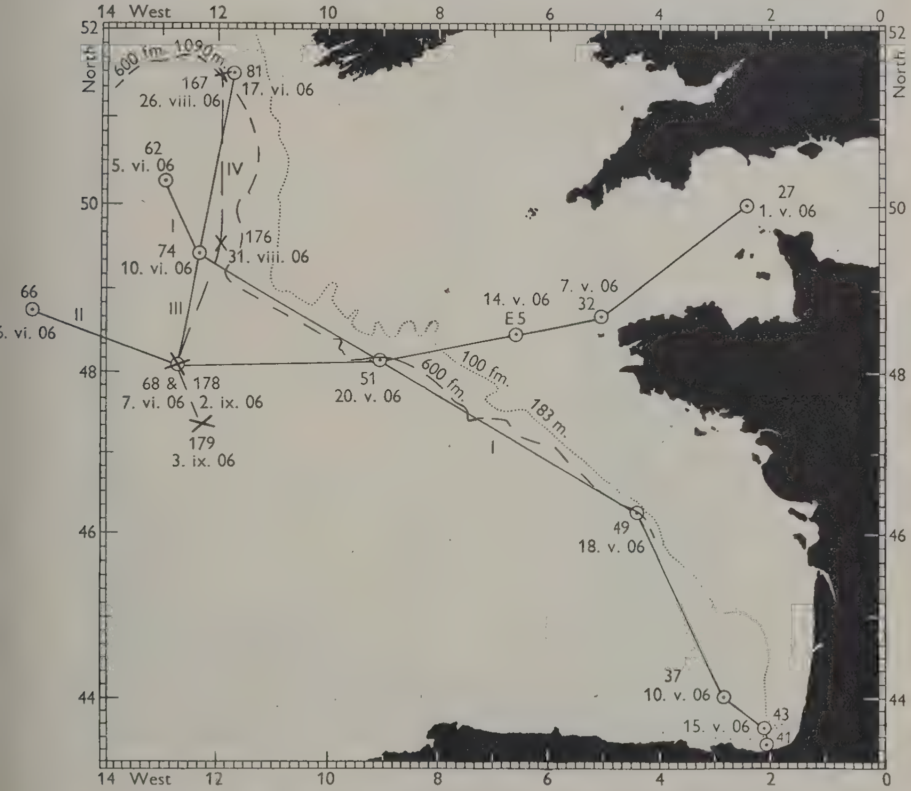
14 West
12
10
8
6
4
2
0
52
50
48
46
44
North
600 fm.
1090 m.
167
26. viii. 06
81
17. vi. 06
62
5. vi. 06
IV
I
74
10. vi. 06
176
31. viii. 06
66
. vi. 06
II
III
68 & 178
7. vi. 06
2. ix. 06
179
3. ix. 06
51
20. v. 06
100 fm.
600 fm.
183 m.
I
14. v. 06
E5
7. v. 06
32
27
1. v. 06
49
18. v. 06
37
10. v. 06
43
15. v. 06
41

Fig. 4. Positions of some stations worked by the Danish research vessel *Thor* in 1906 and the International Hydrographic Station E5.

on 20 May was strongly represented as far north as station 51 (48° 07′ N., 9° 03′ W.), south of the Celtic Sea. Between stations 51 and 74, worked 3 weeks later, a slight bulge in the continental shelf has to be shown in section I. The submarine promontory west of the Little Sole and Great Sole Banks, shown by the 100 and 600 fm. contours on Fig. 4, seems to play a large part in the hydrography of the area and needs constantly to be in mind. In its neighbourhood there seems to have been a marked attenuation in the strength of the Gibraltar water then at station 74 and on other occasions. The continental slope changes in direction from west-north-west to north-north-east and becomes the eastern boundary of a submarine gulf, bight or indentation.[1] If Gibraltar water is to enter this indentation, the water already there must escape either as an eddy in a horizontal plane or by upwelling to levels where movement is less restricted.

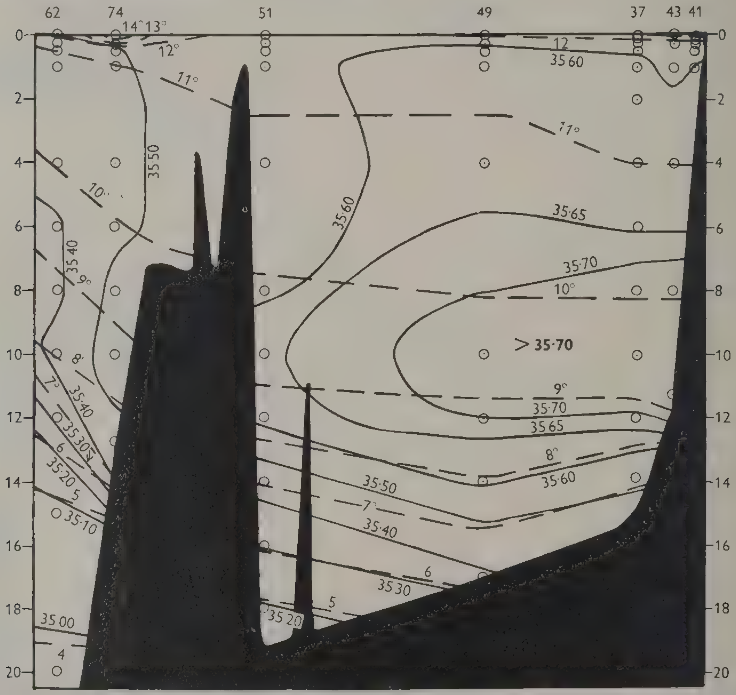

Fig. 5. Section I of Fig. 4 (stations 62–41), based on temperatures and salinities observed by *Thor* between 10 May and 10 June 1906. Bottom topography assessed from Admiralty charts. Depths in hundreds of metres.

Through or around this submarine promontory it is not easy to draw continuous curves for temperature and salinity between stations 51, 74 and 62, spread over 200 miles. The waters north-west and south-east of the 'Sole' submarine promontory evidently have markedly different properties (Fig. 5).

---

[1] The nomenclature of features such as this is at present under discussion. Possible confusion may be avoided by using the term 'indentation', unlikely to be acceptable to anyone as a permanent name for anything. Since it bites into the continental shelf of which the Porcupine Bank is a part it will here, for convenience of repeated reference, be called the 'South Porcupine submarine indentation'.

Section II (Fig. 6) ran down the English Channel and over the continental slope south of the Little Sole Bank, crossing section I at station 51. In the uppermost 400 m. the isopycnals incline downwards away from the continental slope (Fig. 6, inset) suggesting a weak surface current towards the south-east, confirmed from a study of the geopotential topography of the surface against

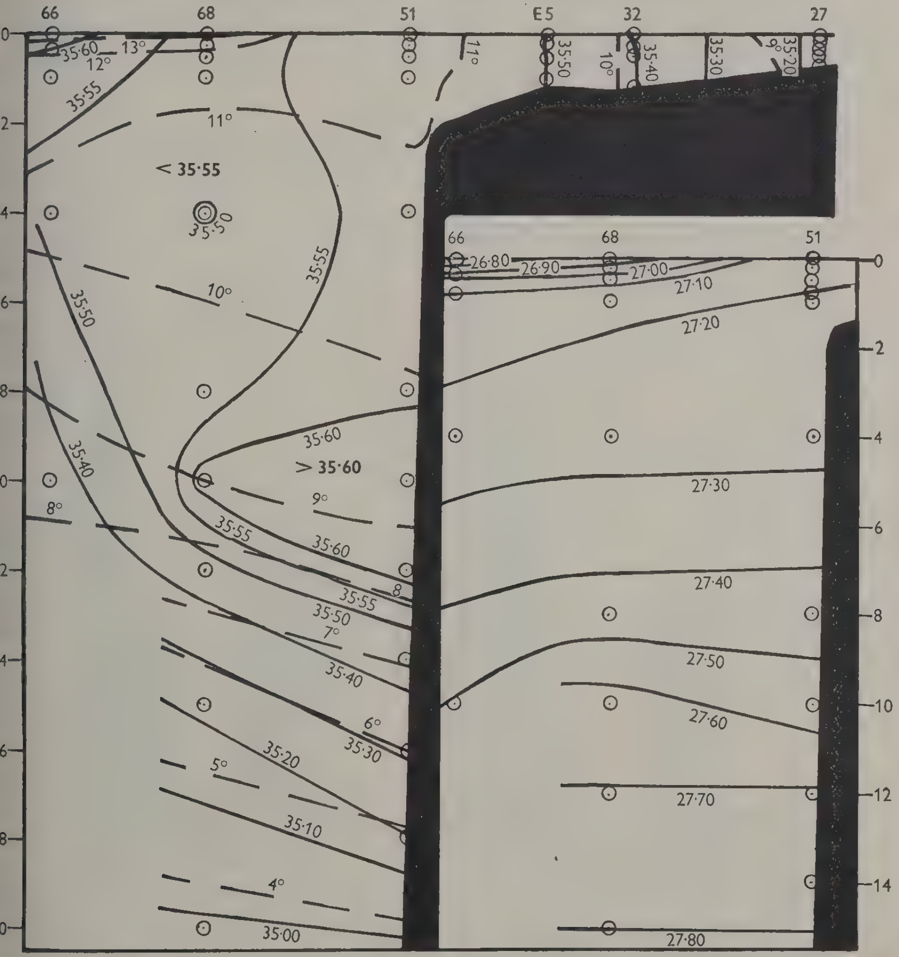

Fig. 6. Section II of Fig. 4 (stations 66–27), based on temperatures and salinities observed by *Thor* between 1 May and 7 June 1906. Inset bottom right, distribution of density ($\sigma_t$). Depths in hundreds of metres.

the 100-decibar surface. Abreast of Ushant the Gulf of Gibraltar water at 1000 m. was held in against the slope and did not extend very far westwards. The slope of the isopycnals for $\sigma_t$ 27·50 and 27·60 suggests that this water mass was still moving west-north-west. Eighty miles off the slope at station 66 the influence of the Gibraltar water was very slight (salinity maximum 35·34 ‰).

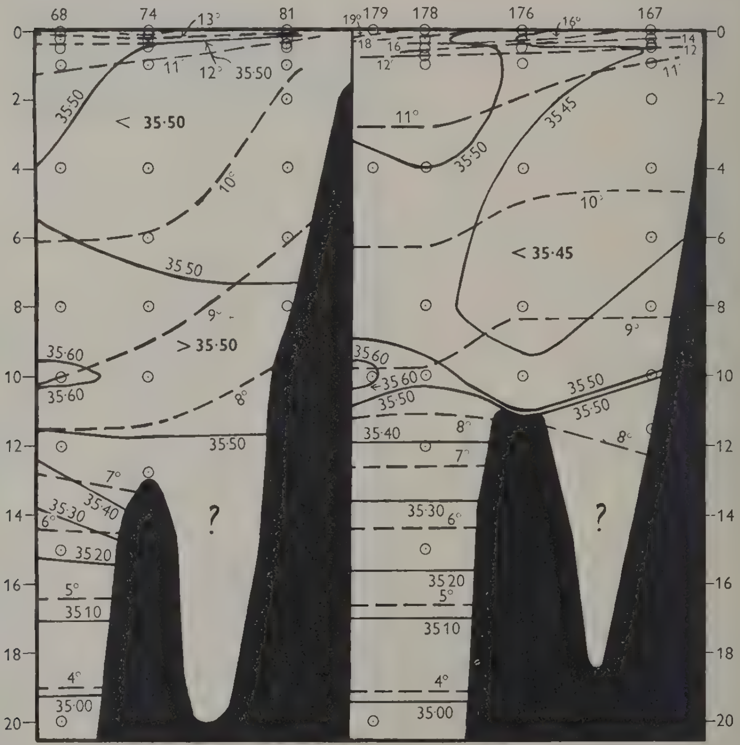

Fig. 7. North-south sections based on temperatures and salinities observed by *Thor*. Section III of Fig. 4 (stations 68, 74, 81), 7–17 June 1906; Section IV (stations 179, 178, 176, 167), 26 August–3 September, 1906. Depths in hundreds of metres.

On the north-south section III (Fig. 7, left), although the water at station 68 undoubtedly included a strong Gibraltar component, one cannot feel the same confidence about the water to the north within the submarine indentation with a salinity of 35·52–35·55 ‰, a temperature of 8·5–9·3° C. and a density $\sigma_t$ of 27·51–27·63. These are compatible with a very considerable proportion of water cascaded from the Rockall Table Mount.

Section IV (Fig. 7, right) shows the change, essentially along section III, in the next 3 months. There had been a marked withdrawal of the saline water at 800–1200 m., causing a decrease in salinity of 0·06–0·10‰. The shape of the surfaces of equal density between stations 178 and 179 (not reproduced) also suggests a south-east-going current at these depths, where the water movements evidently are considerable.

## THE NORTH ATLANTIC DEEP WATER

The deep water of the eastern North Atlantic can only remotely affect the surface water and is of importance to us only for the effect it may have on the stratum of Gulf of Gibraltar water around 1000 m. depth, and as a component of a current system which impoverishes the nutrient regime of the whole of the North Atlantic compared with the other oceans (Sverdrup, Johnson & Fleming, 1942, p. 754).

It is of interest, none the less, that the variations in temperature and salinity of the deep water near the continental slope at the positions italicized in Fig. 8 are quite considerable (Table III). This deep water has been formed, according to Nansen (1912), chiefly at the surface in a limited area south-west of Greenland and to some extent by the outflow from the Norwegian Sea through the bottom of the Faeroe-Shetland Channel (but see Cooper, 1952*b*). According to Helland-Hansen (1930, p. 75) a certain amount of Gulf of Gibraltar water appears to mix downwards to 5000 m.

For the construction of temperature-salinity diagrams in this area the deep water may be characterized by the point *D* having temperature 3·9° and salinity 34·95‰. This point is not quite the same as Jacobsen's (1929) point *B*, derived from and employed for a much wider area.

The distribution of silicate in the deep water is discussed in a separate paper (Cooper, 1952*b*).

## PHOSPHORUS BELOW 1000 M. DEPTH

There have been very few determinations of phosphate in the deep water near the continental slope of the Celtic Sea. On 17–19 June 1930 the *Dana* (*Dana Report*, No. 12, 1937) worked for inorganic phosphate two stations 56 miles south and east respectively of *Discovery II* station 2659 of 12 May 1950. The *Dana* results (Table IV) have been multiplied by 1·35 to correct for salt error (Cooper, 1938*b*). They may be compared with the *Discovery II* results for total phosphorus which would be expected to be about 0·1 $\mu$g.-atom/l. greater. Actually below 1200 m. depth they were about 0·2 $\mu$g.-atom/l. less, a notable result if it is correct. The following comments may be made:

(i) Although, for reasons to be given (Appendix, p. 509), the accuracy of the analyses made on the *Discovery II* samples is not very high, there is little reason to doubt their accuracy to one decimal place as reported.

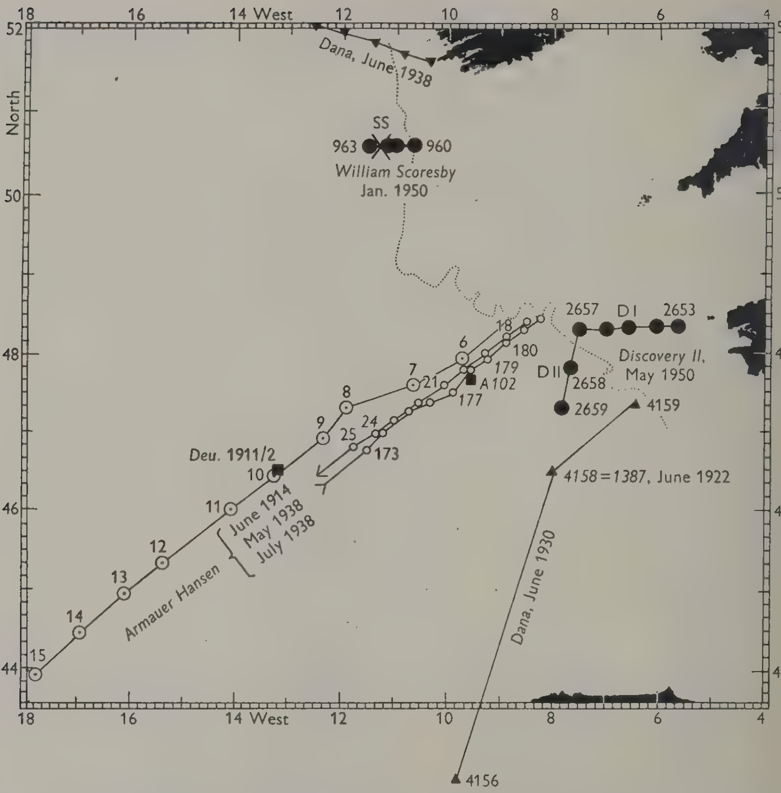
18
16
14 West
12
10
8
6
4
52
50
48
46
44
North
Dana, June 1938
SS
963
960
William Scoresby
Jan. 1950
2657
D I
2653
Discovery II,
May 1950
D II
2658
2659
4159
4158 = 1387, June 1922
Dana, June 1930
4156
18
180
179
177
A 102
6
7
21
8
9
24
25
173
Deu. 1911/2
10
11
12
13
14
15
June 1914
May 1938
July 1938
Armauer Hansen

Fig. 8. Positions of deep stations off the continental slope of the Celtic Sea: ⊙, *Armauer Hansen* stations in June 1914; ○, *Armauer Hansen* stations in May and July 1938; ▲, *Dana* stations in June 1930 and one in June 1922; ▼, *Dana* stations in June 1938; ■, *Deutschland* Reihe 2 in May 1911 and *Altair* station 102 in July 1938; ●, stations by R.R.S. *William Scoresby* in January 1950 and by R.R.S. *Discovery II* in May 1950; ×, position of the Irish station SS.

TABLE III. RANGE OF TEMPERATURES AND SALINITIES RECORDED AT THE DEEP STATIONS ITALICIZED ON FIG. 8

| Depth (m.) | $\Delta T$ (° C.) | $\Delta S$ (‰) |
|---|---|---|
| 2000 | 0·6 | 0·09 |
| 2500 | 0·3 | 0·07 |
| 3000 | 0·1 | 0·04 |
| 3500 | 0·05 | 0·04 |

(ii) Although Dr H. Thomsen and Dr A. Fr. Bruun, the skilful observers who made the analyses at sea on board *Dana*, make no high claim for the accuracy of their inorganic phosphate analyses, an error of greater than ± 0·1 μg.-atom/l. seems unlikely.

(iii) The salt error correction factor is not a true constant, but only a factor less than 1·1 could make the deep water results consistent. Such a factor was highly unlikely.

TABLE IV. VERTICAL DISTRIBUTION OF PHOSPHORUS (μG.-ATOM/L.) IN THE BAY OF BISCAY IN 1930 AND 1950. INORGANIC PHOSPHATE OR TOTAL PHOSPHORUS

| Ship ... | *Dana* | *Dana* | *William Scoresby* | | *Discovery II* |
|---|---|---|---|---|---|
| Station no. ... | 4158 | 4159 | 963 | | 2659 |
| Lat. N. ... | 46° 28′ | 47° 20′ | 50° 34′ | | 47° 24′ |
| Long. W. ... | 8° 01′ | 6° 28′ | 11° 30′ | | 7° 52′ |
| Date ... | 17. vi. 30 | 19. vi. 30 | 19. i. 50 | | 12. v. 50 |
| Depth (m.) | Inorganic phosphate | Inorganic phosphate | Inorganic phosphate | Total phosphorus | Total phosphorus |
| 100 | 0·5$_7$ | 0·5$_7$ | 0·55 | 0·70 | 0·5 |
| 150 | 0·6$_7$ | 0·5$_7$ | 0·53 | — | 0·6 |
| 200 | 0·7$_6$ | 0·5$_7$ | 0·54 | 0·70 | 0·6 |
| 300 | 0·6$_7$ | 0·6$_7$ | 0·65 | — | 0·8 |
| 400 | 0·7$_6$ | 0·7$_6$ | 0·75 | 0·93 | 0·8 |
| 500 | 0·9$_5$ | 0·9$_5$ | 0·96 | — | — |
| 600 | 1·1$_4$ | 1·0$_5$ | 0·97 | 1·08 | 1·0 |
| 800 | 1·1$_4$ | 1·1$_4$ | 1·13 | 1·26 | 1·3 |
| 900 | — | — | 1·13 | 1·33 | 1·2 |
| 1000 | 1·1$_4$ | 1·1$_4$ | 1·17 | 1·30 | 1·2 |
| 1100 | — | — | 1·20 | 1·33 | 1·3 |
| 1200 | 1·2$_3$ | — | 1·19 | 1·33 | 1·2 |
| 1500 | 1·5$_2$ | — | — | — | 1·3 |
| 2000 | 1·5$_2$ | — | — | — | 1·3 |
| 2500 | 1·7$_1$ | — | — | — | 1·4 |
| 3000 | 1·8$_0$ | — | — | — | 1·6 |
| 3500 | 1·8$_0$ | — | — | — | 1·5 |
| 3800 | — | — | — | — | 1·6 |
| 4000 | 1·8$_0$ | — | — | — | — |
| 4500 | 1·9$_0$ | — | — | — | — |

(iv) The *Dana* results at stations 4158 and 4159 between 400 and 1200 m. agree closely with the relatively accurate analyses for inorganic phosphate made 20 years later on *William Scoresby* samples from a position about 280 miles to the north-north-west (Table IV).

(v) The *Dana* results of a week earlier at station 4149, 11 miles off Cape Espichel, Portugal, below the productive zone, lie within the range of variation of inorganic phosphate established in the neighbourhood by Bôto (1945; also in Cons. Int., *Bull. Hydrogr.* for 1934) on the Portuguese research vessel *Albacora* 4 years later (Table V).

(vi) The *Dana* results in 1930 show a steady increase in inorganic phosphate at 1000–2000 m. from the neighbourhood of Lisbon northwards to the border of the Celtic Sea (Table VI).

(vii) The *Discovery II* results between 200 and 1300 m. check well with the more accurate analyses of total phosphorus made on *William Scoresby* samples from a position about 280 miles to the north-north-west in the same year 1950 (Table IV).

TABLE V. COMPARISON OF INORGANIC PHOSPHATE CONTENT (AS $\mu$G.-ATOM/L. P) AT *DANA* STATION 4149, 11 MILES OFF CAPE ESPICHEL (NEAR LISBON) WITH *ALBACORA* STATIONS WITHIN 22 MILES OF IT, AND WITH *ALBACORA* STATION 558

| Ship ... | *Albacora* | | | *Dana* | *Albacora* | | *Albacora* |
|---|---|---|---|---|---|---|---|
| Station no. ... | 442 | 486 | 488 | 4149 | 448 | 556 | 558 |
| Lat. N. ... | 38° 26′ | 38° 27′ | 38° 27′ | 38° 19′ | 38° 17′ | 38° 15′ | 39° 29·5′ |
| Long. W. ... | 9° 30′ | 9° 28′ | 9° 20′ | 9° 26′ | 9° 13′ | 9° 10′ | 9° 37·5′ |
| Date ... | 8. ii. 34 | 9. v. 34 | 9. v. 34 | 11. vi. 30 | 9. ii. 34 | 14. viii. 34 | 17. viii. 34 |
| Depth (m.) | | | | | | | |
| 300 | — | 0·58 | 0·70 | $0{\cdot}7_7$ | — | 0·79 | — |
| 400 | 0·79 | 0·77 | 0·80 | $0{\cdot}8_5$ | 0·62 | 0·80 | 0·68 |
| 500 | — | — | — | $0{\cdot}9_5$ | — | 0·87 | — |
| 600 | — | 0·70 | 0·80 | $0{\cdot}5_7$ | — | 0·78 | 0·79 |
| 800 | 0·86 | 0·69 | 0·83 | $0{\cdot}5_7$ | 0·55 | 0·79 | 0·66 |
| 1000 | 0·70 | 0·75* | — | $0{\cdot}5_7$ | 0·62 | — | 0·59 |
| 1200 | 0·70 | 0·83* | — | $0{\cdot}8_5$ | 0·62 | — | 0·68 |
| 1300 | — | 0·89 | — | — | — | — | — |
| 1400 | — | — | — | — | — | — | 0·96 |
| 1500 | — | — | — | $0{\cdot}9_5$ | — | — | — |
| 1600 | — | — | — | — | — | — | 0·96 |

* Interpolated with 900 m. result.

TABLE VI. INORGANIC PHOSPHATE (AS $\mu$G.-ATOM/L. P) AT *DANA* STATIONS BETWEEN 1000 AND 2000 M. DEPTH

| *Dana* station ... | 4148 | 4149 | 4156 | 4158 | 4159 |
|---|---|---|---|---|---|
| Lat. N. ... | 37° 02′ | 38° 19′ | 42° 41′ | 46° 28′ | 47° 20′ |
| Long. W. ... | 9° 17′ | 9° 26′ | 9° 49′ | 8° 01′ | 6° 28′ |
| Date ... | 11. vi. 30 | 11. vi. 30 | 16. vi. 30 | 17. vi. 30 | 19. vi. 30 |
| Depth (m.) | | | | | |
| 1000 | $0{\cdot}6_7$ | $0{\cdot}5_7$ | $1{\cdot}0_5$ | $1{\cdot}1_4$ | $1{\cdot}1_4$ |
| 1200 | $0{\cdot}7_6$ | $0{\cdot}8_5$ | $1{\cdot}0_5$ | $1{\cdot}2_3$ | — |
| 1400 | $0{\cdot}9_5$ | — | — | — | — |
| 1500 | — | $0{\cdot}9_5$ | $1{\cdot}3_8$ | $1{\cdot}5_2$ | — |
| 1600 | $1{\cdot}2_4$ | — | — | — | — |
| 2000 | — | — | $1{\cdot}3_3$ | $1{\cdot}5_2$ | — |

(viii) It would seem therefore that in the northern Bay of Biscay in June 1930 the phosphate content at 1200–2000 m. was higher than it is now in the same area or than it was then to the southward. Variations in phosphate content of at least 0·2 $\mu$g.-atom/l. have taken place. It may not be by chance that the decrease in the deep water has occurred at the same time as that in the English Channel near Plymouth.

### North Atlantic Central Water

According to Sverdrup *et al.* (1942, p. 668) North Atlantic Central water characterized by a nearly straight $T$–$S$ curve between $T=8°$, $S=35{\cdot}10‰$ and $T=19°$, $S=36{\cdot}70‰$ has been found over a very large area of the North Atlantic. In this area its presence has been masked below 10° and above 11·5° C. Below 10° its place is taken by Gulf of Gibraltar or cascade waters. Above 11·5° we find the zone of strong seasonal variations, due to solar heating of the surface waters in summer and of vertical mixing in winter. Between these limits occurs water resembling the Central water but, rather surprisingly, somewhat warmer, and needing its own $T$–$S$ curve. This can be derived only from stations where oxygen determinations are available, such as stations 7–15 of *Armauer Hansen* in 1914. Those selected were:

| Station *AH* 1914 ... | 15 | 13 | 12 | 10 | 9 | 8 | 7 |
|---|---|---|---|---|---|---|---|
| Depth range used (m.) | 100–700 | 75–400 | 100–600 | 75–200 | 100–400 | 200–500 | 400 only |

The linear $T$–$S$ curve so calculated is

$$S=35{\cdot}50_8+0{\cdot}124(T-11). \qquad (2)$$

The temperature and salinity of North Atlantic Central water below 100 m. depth brought into this area should comply with this relation (see Fig. 9).

### *The Upper Limit of Central Water*

The upper limit of North Atlantic Central Water is the point where the $T$–$S$ curve ceases to follow equation (2). In winter and spring the upper waters are homogeneous, represented by a point, and in summer they are isohaline and represented by a vertical $T$–$S$ curve. In June 1914 at the *Armauer Hansen* stations the upper limit was clearly definable within 25 m. (Table VII).

Table VII. The Upper Limit of North Atlantic Central Water at *Armauer Hansen* Stations 15 to 6 in June 1914

| Station ... | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 |
|---|---|---|---|---|---|---|---|---|---|---|
| Depth of upper limit (m.) | 100 | 75 | 75 | 100 | *c.* 75 | 100* | 100 | 200 | 200 | Not present |
| Temperature (° C.) | 12·37 | 12·50 | 12·59 | 11·53 | 11·27 | 11·64 | 11·02 | 11·10 | 10·93 | |
| Salinity (‰) | 35·69 | 35·69 | 35·72 | 35·59 | 35·54 | 35·57 | 35·51 | 35·55 | 35·53 | |
| Oxygen (%) | 92 | 93 | 92·5 | 96 | 98 | 94 | 96 | 95 | — | |

* High oxygen content (104%) shows that the 75 m. water belonged within the zone of winter mixing, not of Central Water.

From station 15 inwards to station 9, as at many other deep Atlantic stations, the limit of vertical mixing had been between 75 and 100 m. depth (Fig. 9). Moreover, at the more seaward stations 15, 14 and 13, the winter surface water had had a salinity of about 35·70‰ and a temperature of 12·4–12·6° C. Chemically it was essentially the same water as that underlying it.

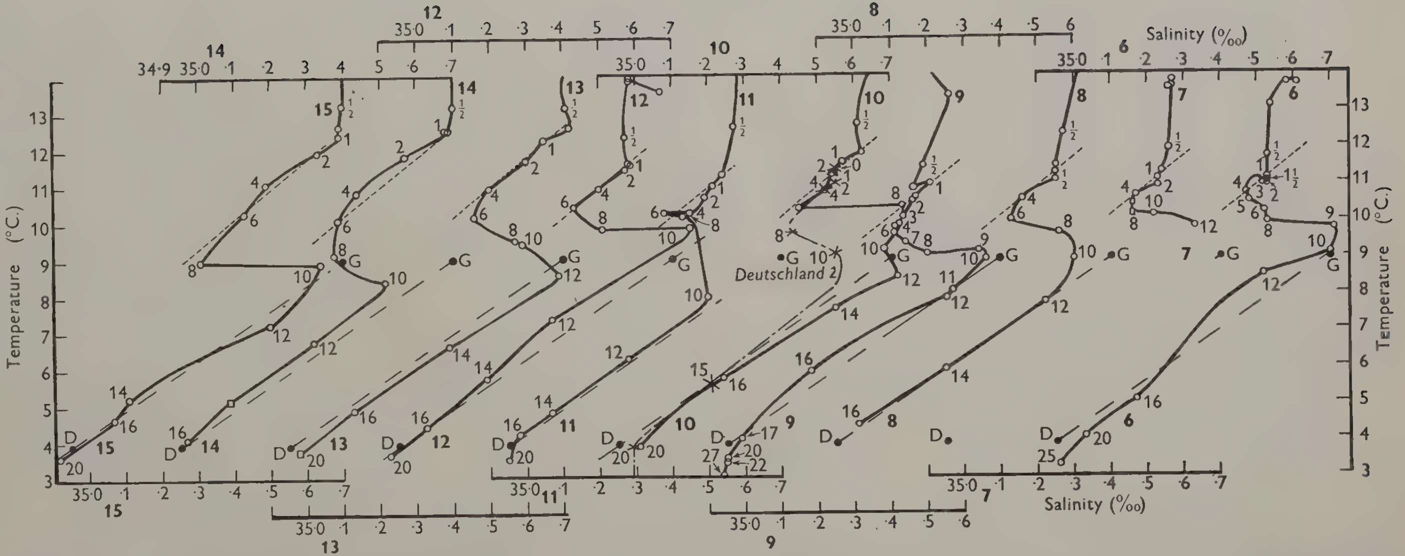

Fig. 9. Temperature-salinity relationships for *Armauer Hansen* stations 15–6 (see Fig. 8 for positions) worked in June 1914. The linear curves representing the properties of mixed Gulf of Gibraltar and Deep water (equation 1, p. 467) and North Atlantic Central water (equation 2, p. 479) are indicated by dashed and dotted lines respectively. *Deutschland* Reihe 2 is superimposed on *Armauer Hansen* station 10, from which it was distant about four miles. The points G and D represent the mean properties of Gulf of Gibraltar and North Atlantic Deep Water. The figures in bold-faced type denote station numbers. The remaining numbers against the curves denote depths of observations in hundreds of metres.

Approaching the continental slope at stations 8, 7 and 6 the apparent depth of vertical mixing was more than twice as great (Fig. 9). Meteorological conditions at these stations cannot have differed greatly from those farther out, and one is forced to seek another origin for the upper 200–300 m. of water with salinity between 35·51 and 35·55 ‰ and temperature between 10·9 and 11·1° C. We have to deal with a phenomenon peculiar to the neighbourhood of the continental slope (cf. Cooper, 1952*a*).

### *The Lower Limit of Central Water*

The lower limit of the North Atlantic Central water rises as the continental slope is approached (Table VIII).

TABLE VIII. THE LOWER LIMIT OF NORTH ATLANTIC CENTRAL WATER AT *ARMAUER HANSEN* STATIONS 15 TO 6 IN JUNE 1914

| Station ... | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 |
|---|---|---|---|---|---|---|---|---|---|---|
| Depth of lower limit (m.) | 750 | 500 | 500 | 600 | 400? | 400? | 500 | 500 | 400 | Not present |
| Temperature (° C.) | 9·35 | 10·40 | 10·55 | 10·34 | 10·25 | 10·82 | 9·90 | 10·32 | 10·69 | |
| Salinity (‰) | 35·33 | 35·41 | 35·47 | 35·43 | 35·45 | 35·52 | 35·41 | 35·43 | 35·47 | |
| Oxygen (%) | *c.*73 | 84 | 82 | 85 | 85·5 | 86·5 | 84·5 | 81 | 83 | |

It extends down to 750 m. at station 15 and only to 400 m. at station 7. At station 6 it is not recognizable in the midst of more highly oxygenated water. It was underlain either by a mixed water formed between itself and Gulf of Gibraltar water as at stations 15, 14, 13, 12, 9 and 8 or by cascaded water as at stations 11, 10 and 7.

The stratum of Central water gets thinner as the slope is approached (Figs. 9 and 11). At station 15 it was 700 m. thick, whereas it was recognizable with certainty at station 7 only at 400 m. Evidently, in June 1914, the North Atlantic Central water had little direct effect on the Celtic Sea.

At the upper limit the Central water has an oxygen content 92–98 % saturated, at the lower 81–85 %. The high oxygen content (99 %) at stations 6 at 400 m. shows that this was not Central but 'capsized' or cascaded water. The temperature, salinity and density were appropriate to Celtic Sea water the previous winter. The arrival of cascade water in the ocean abreast of the slope may bring about a state of labile or metastable equilibrium to a considerable depth. Winds, which can mix the waters of the open ocean only to 75–100 m., can therefore with the same ease homogenize the waters near the slope by a 'capsizing' process (Cooper, 1952*a*) to a much greater depth.

## SUBMARINE VALLEYS IN THE CONTINENTAL SLOPE

In February 1949 a survey of an area around 48° N. lat., 9° 30′ W. long. was carried out in good weather by the present Hydrographer of the Navy, Rear-Admiral A. Day, C.B.E., D.S.O., when in command of H.M. Surveying

Ship *Dalrymple*. The whole survey, based on a floating beacon anchored near the 100 fm. line and fixed by a series of star sights, was achieved by echo-sounding checked by the lead at intervals. A portion of the resulting document has been reproduced here (Fig. 10) by permission of the Hydrographer of the Navy.

If the sea-level were to fall by several hundred fathoms, a ria coast of strong relief would stand revealed. Thus the submarine valley at 48° 13′ N., 9° 21′ W. cuts back for about 9 sea miles (17 km.) and sections across it show that the maximum depth of the valley bottom below the containing spurs is about 1800 ft. (550 m.).

The French research vessel *Président Théodore Tissier* (Beaugé, 1934) has charted the continental slope between 48° 10′ N. lat., 9° 20′ W. long. and 49° 00′ N. lat., 11° 10′ W. long. I am much indebted to Monsieur P. Desbrosses for presenting me with a copy of this chart. The area surveyed was much greater and the density of soundings would seem to have been less, possibly considerably less, than in *Dalrymple's* survey so that the contoured chart is likely to be less accurate in detail than that reproduced in Fig. 10. However, great detail is not necessary to show that to the west-north-west there are a number of submarine canyons of even greater size. Thus the steep cliff shown in Fig. 10 (top left) would appear to be one jaw of a canyon about 15 miles long and with a maximum depth between and below the containing spurs of about 4000 ft. This canyon and others appear to be ideally shaped to create submarine eagres whilst the broad spurs shown in Fig. 10 and two similar ones at 48° 40′ N., 10° 22′ W. and 48° 35′ N., 10° 10′ W. appear likely to exacerbate the capsizing process suggested as occurring in southerly gales all along the continental slope. Continuous and extensive observations over these submarine canyons would be needed before well-placed standard hydrographical stations off the continental slope between 6 and 11° W. can be proposed.

## THE VERTICAL DISTRIBUTION OF WATER MASSES

Making use of the extensive information to be gleaned from Fig. 9 and from the sections and plots for temperature, salinity and density by Helland-Hansen & Nansen (1927, table II and plates 14 and 32) and from those for oxygen by Gaarder (1927, pp. 9–14, and Schnitt 1*a* and *b*), it is possible to identify the several water masses in the *Armauer Hansen* section in June 1914 (Fig. 11). It is not possible to assess the importance of internal waves in causing the undulating boundaries, particularly of the Gulf of Gibraltar water. At station 11 this was completely squeezed out so that the Celtic Cascade Core (see below) and the Mixed Gibraltar-Deep water were in contact.

Station 15 was a typical and simple oceanic station with North Atlantic Central and Gulf of Gibraltar water clearly developed.

Stations 11 and 10 exhibited marked idiosyncrasies. At 800 m. at station 11 and at 600 m. at station 10 was a core of highly oxygenated water (Table IX, italicized), having properties appropriate to the north-western Celtic Sea the previous winter. There is little doubt that it had recently cascaded and had been forced out into the ocean as a core (cf. Cooper & Vaux, 1949), having been canalized in a submarine valley such as those shown in Fig. 10. The

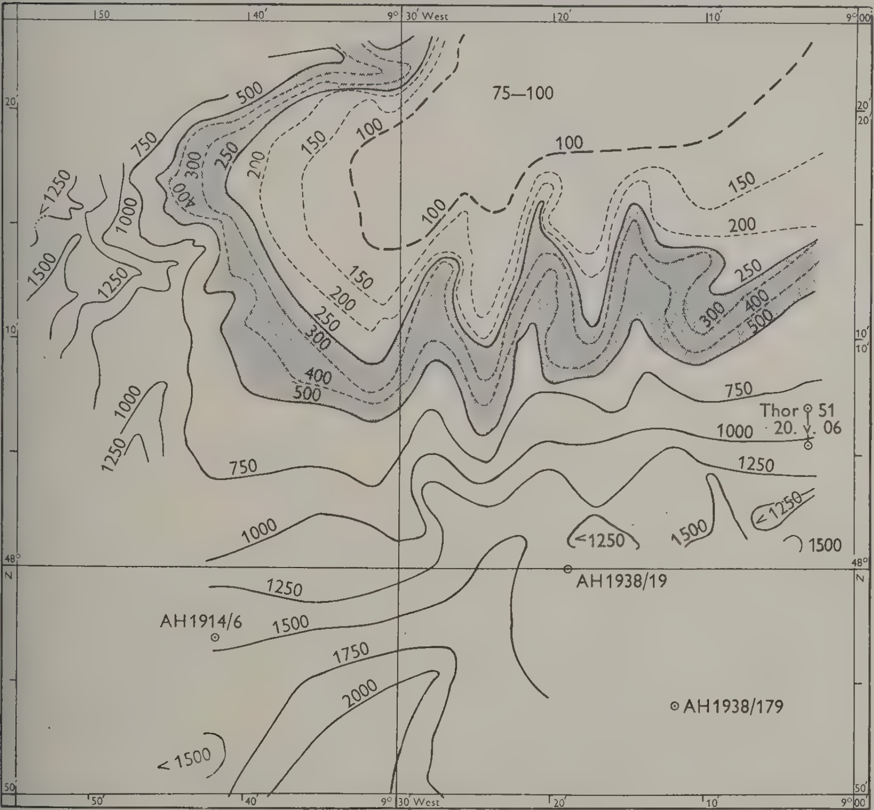

Fig. 10. Contoured bottom topography of the continental slope of the Celtic Sea in the neighbourhood of 48° N. lat., 9° 30′ W. long., making use, by permission of the Hydrographer of the Navy, of an original hydrographic survey carried out by H.M. Surveying Ship *Dalrymple* (Captain, now Rear-Admiral A. Day, C.B.E., D.S.O.) in February 1949. South of 48° N. lines of soundings are comparatively few. The contours at 250 and 1750 fm. have been added by the author. The 100 fm. contour is shown by a thick broken line. Contours at 250 fm. intervals are shown by thick continuous lines. Intermediate contours at 50 fm. intervals from 100 to 300 fm. and at 400 fm. are shown by thin dotted lines. The slope between the 250 and 500 fm. contours is stippled. The positions of the important station 6 worked by *Armauer Hansen* in June 1914 and of two stations worked by the same ship in 1938 are shown. The position of station 51, worked by *Thor* on 20 May 1906, is marked by an open circle, together with the adjustment necessary to bring the sounding reported by *Thor* into line with the chart.

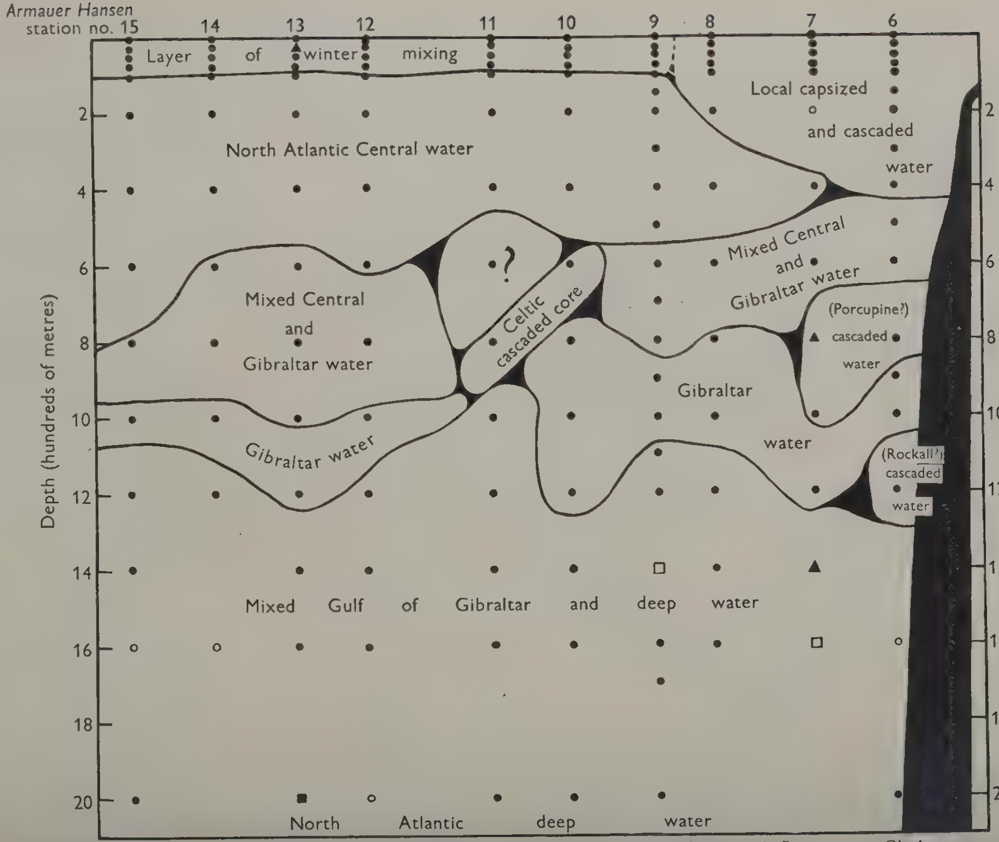

Fig. 11. Section illustrating distribution of water masses at *Armauer Hansen* stations 15–6, June 1914. Circles represent determinations of temperature and salinity, squares represent determinations of temperature only, and triangles of salinity

stability at the base of the core ($\Delta\sigma_t$ 0·41 in 200 m.) was remarkable. The core almost certainly originated north of the *Armauer Hansen* section, so that the fact that the oxygen-rich water lay deeper at the outer station no. 11 than at no. 10 agrees with a thesis, propounded by Sandström (1918, p. 241) and confirmed by other work at Plymouth, that such currents move forward in the northern hemisphere with a right-handed-screw motion.

The position of station 10 was within 5 miles of that of *Deutschland* Reihe 2 (46° 29′ N., 13° 11′ W.) on 16 May 1911, the temperature-salinity relation for which has been superimposed on Fig. 9 (Station 10) as a fine dashed and dotted line. The nature of the water masses on the two occasions differed greatly but, unfortunately, no depth was worked between 400 and 800 m. or between 1000 and 1500 m.

TABLE IX. CORE OF CELTIC SEA CASCADE WATER OBSERVED BY *ARMAUER HANSEN* ON 7 JUNE 1914

| Depth (m.) | Oxygen | | Salinity (‰) | Temp. (° C.) | Density $\sigma_t$ | Nature of water |
|---|---|---|---|---|---|---|
| | (cc./l.) | % | | | | |
| Station 11, 46° 00′ N., 14° 03′ W. | | | | | | |
| 400 | 5·45 | 85·$_5$ | 35·45 | 10·25 | 27·28 | North Atlantic Central |
| 600 | 4·83 | 76 | 35·38 | 10·24 | 27·22 | ? |
| *800* | *5·48* | *86* | *35·43* | *10·17* | *27·28* | *Celtic Cascade Core* |
| 1000 | 4·55 | 68 | 35·50 | 7·95 | 27·69 | Mixed Gulf of Gibraltar and Deep |
| Station 10, 46° 25′ N., 13° 14′ W. | | | | | | |
| 400 | 5·44 | 86·$_5$ | 35·52 | 10·82 | 27·23 | North Atlantic Central |
| *600* | *6·01* | *94·$_5$* | *35·45* | *10·36* | *27·26* | *Celtic Cascade Core* |
| 800 | 4·07 | 64·$_5$ | 35·73 | 10·44 | 27·48 | Gulf of Gibraltar |
| 1000 | 4·38 | 67·$_5$ | 35·68 | 9·25 | 27·63 | Gulf of Gibraltar |

At station 6 against the slope, North Atlantic Central water was not recognizable and only vestigially at 400 m. at station 7. Gulf of Gibraltar water was present strongly at 900–1000 m. at station 6 and at 1200 m. at station 7.

Also at station 6 oxygenated water was banked against the slope in three separate strata. That above 400 m. depth was largely a mixed water formed by cascading from the continental shelf and by capsizing over the continental slope. For the highly oxygenated water at 800 m., there may be no need to seek an origin farther north than cascade water from the Porcupine Bank. That at 1200 m., beneath the Gulf of Gibraltar water, may have cascaded from the neighbourhood of the Rockall Table Mount, an event which will be further discussed below (p. 497, and Table XVIII). To these several water masses of very different histories but similar salinities, it is considered very probable that some organisms may react very differently, particularly at sensitive stages in their life histories, such as development of diatom resting spores, fertilization and hatching of eggs and moulting of crustaceans (cf. Wilson, 1951). Therefore, when discussing the hydrographical background of biological events it is never sufficient to speak of 'an influx of Atlantic Water'. The particular kind of Atlantic water needs to be identified.

## RESULTS OF THE INTERNATIONAL GULF STREAM EXPEDITIONS 1938

In June 1938 a section with stations 20 miles apart was worked by the Danish research vessel *Dana* from 51° 33′ N., 10° 22′ W. off Dursey Head, County Kerry, to 53° 48′ N., 20° 21′ W. (Fig. 8) (Cons. Int., *Bull. Hydrogr.* for 1938). The section crossed the submarine indentation and the southern spur of the Porcupine Bank into the deeper Eastern North Atlantic. The distribution of properties was complex and their interpretation will be difficult. Two similar but less complex sections were worked at the same time by the Norwegian vessel *Armauer Hansen*, south-west from the English Channel towards the Azores. No advantage is to be gained by a superficial examination of these valuable observations. Their application to our problems, especially to the Celtic Sea mackerel investigations in the same year, is deferred until the Scandinavian oceanographers have published their conclusions.

## THE SLOPE WATERS OFF THE CELTIC SEA IN 1950

On 18–19 January 1950, R.R.S. *William Scoresby* worked four stations along the parallel 50° 34′ N. between 10° 40′ and 11° 30′ W. (Fig. 8), where the results of the Irish investigations at station SS (50° 34′ N., 11° 17′ W.) had shown that vertical exchanges occur. Later, on 11–12 May, R.R.S. *Discovery II* worked a line of three stations (section D II) over the slope between 48° 18′ N., 7° 30′ W. and 47° 24′ N., 7° 52′ W., the deepest being sampled to 3800 m. depth. She worked other stations on the shelf, which will be discussed in a later paper. Cordial thanks are due to Dr G. E. R. Deacon, F.R.S., and to Dr N. A. Mackintosh for arranging this co-operation, to Dr T. J. Hart and Dr H. P. F. Herdman, scientists in charge of the two ships, and to Mr R. I. Currie and Mr H. Cox, who were responsible for collecting many of the samples, and to Mr Currie for the analyses of oxygen. The results are presented graphically in Figs. 12–15.

The vertical variations in salinity and temperature between the surface and 1200 m. depth (Fig. 12) are smaller than in most parts of the world, but are characteristic of the waters bathing the Western European continental slope between Gibraltar and Western Ireland. Within this framework there is a very marked difference in the nature of the water masses encountered on the two cross-slope sections.

### *The Surface Waters*

On the northern section worked by R.R.S. *William Scoresby* on 18–19 January 1950 vertical mixing was apparent down to 250 m., as on the *Armauer Hansen* section in June 1914 (Figs. 9, 12 and 13, panel 3). Along the 33-mile long section the distribution of density above 250 m. depth was almost uniform (27·05–27·11 $\sigma_t$), indicating very sluggish water movements parallel to the continental slope and the results of capsizing. None the less the total phosphorus content showed a horizontal increase westward of about 0·1 μg.-atom/l. as the brim of the slope was crossed (Fig. 13, panel 4). Again, in spite of the generally vertically uniform temperature distribution, there were small density inversions which appear to be real at 20, 150 and 300 m. (Fig. 12). This phenomenon, frequently observed in this neighbourhood, will be discussed in another paper.

The content of nutrients at the easternmost station WS960 (50° 34′ N., 10° 40′ W.; total phosphorus 0·61–0·63, inorganic phosphate 0·48–0·53 μg.-atom/l. P) suggested that some areas of the northern Celtic Sea were little richer than the English Channel.

The phosphate content on 19 February 1927 at position SS, determined by Atkins (1928), may be compared with that at the same position and depths interpolated from stations WS962 and 963 (Table X).

TABLE X

| Depth (m.) | 19 February 1927 | 18–19 January 1950 |
|---|---|---|
| 0 | 0·46 | 0·55 |
| 402 | 0·72 | 0·73 |
| 860 | 0·91 | 1·13 |

The difference between the two water masses on the sections worked by R.R.S. *William Scoresby* in the north and R.R.S. *Discovery II* in the south shows up most clearly on a temperature-salinity diagram (Fig. 15). At no depth are the two waters closely related.

Along the southern (D II) section in May there was no relict isothermal, isopycnal layer remaining to indicate the lower limit of vertical mixing during the winter. It is unlikely that it extended down to 300 m. The contents of total phosphorus and of silicate-Si of the uppermost 100 m. (0·3–0·6 and 0·5–2·2 μg.-atom/l. respectively (Fig. 14, panels 4 and 5) were or had become low. It is probable that the relatively nutrient-rich winter surface water here (which should have been created by the gales of the first week of February) had been replaced by impoverished surface water from the ocean to the south or from the Biscayan shelf. If later such water moved into the English Channel it could bring only poor conditions with it.

In the southern section in May there was a density gradient (Fig. 14, panel 3). Assuming only horizontal water movements, this would indicate a weak eastbound current flowing along the edge of the slope, in agreement with the current system already deduced for the region by Helland-Hansen and Nansen (1927); but since vertical currents and internal waves may also have played a part no firm conclusion is possible. At least it seems that the impoverished warm saline surface water is more likely to have come from the ocean to the south-west or west than from the Biscayan shelf to the south-east.

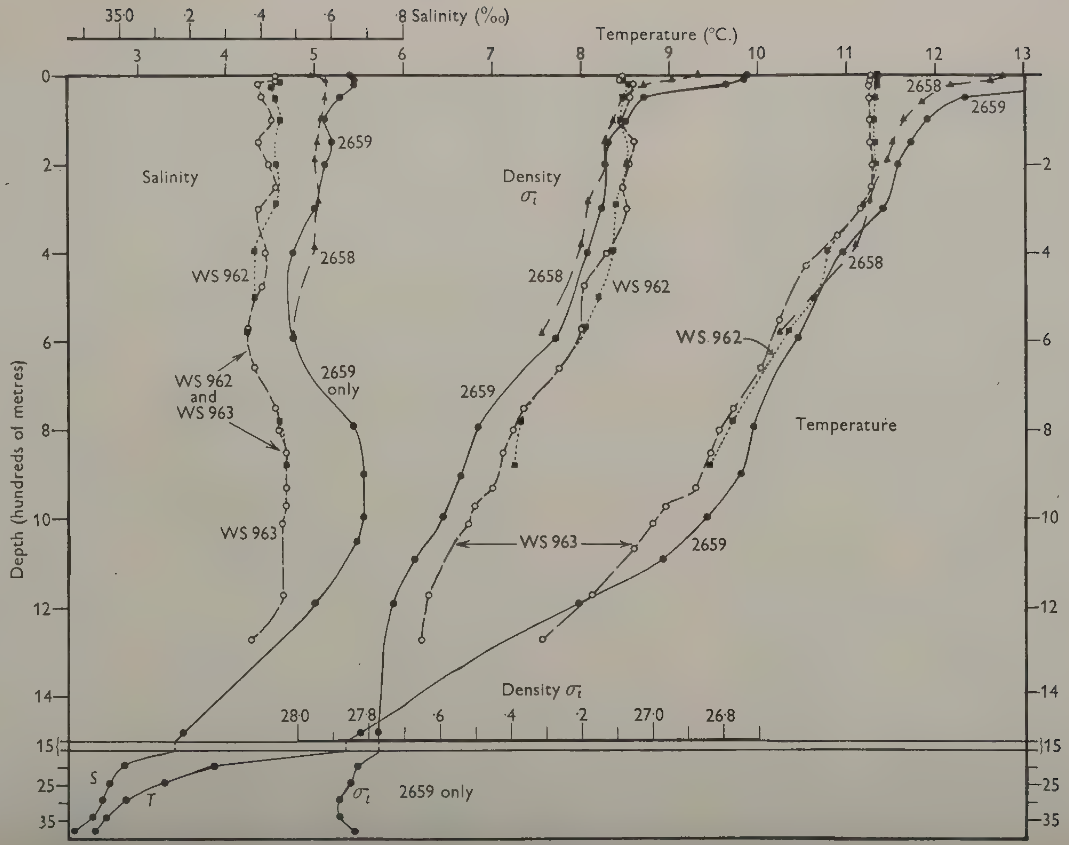

Fig. 12. Vertical distribution of salinity, density and temperature at *William Scoresby* stations 962 (···■···), 963 (---○---) on 18–19 January 1950, and *Discovery II* stations 2658 (——▲——) and

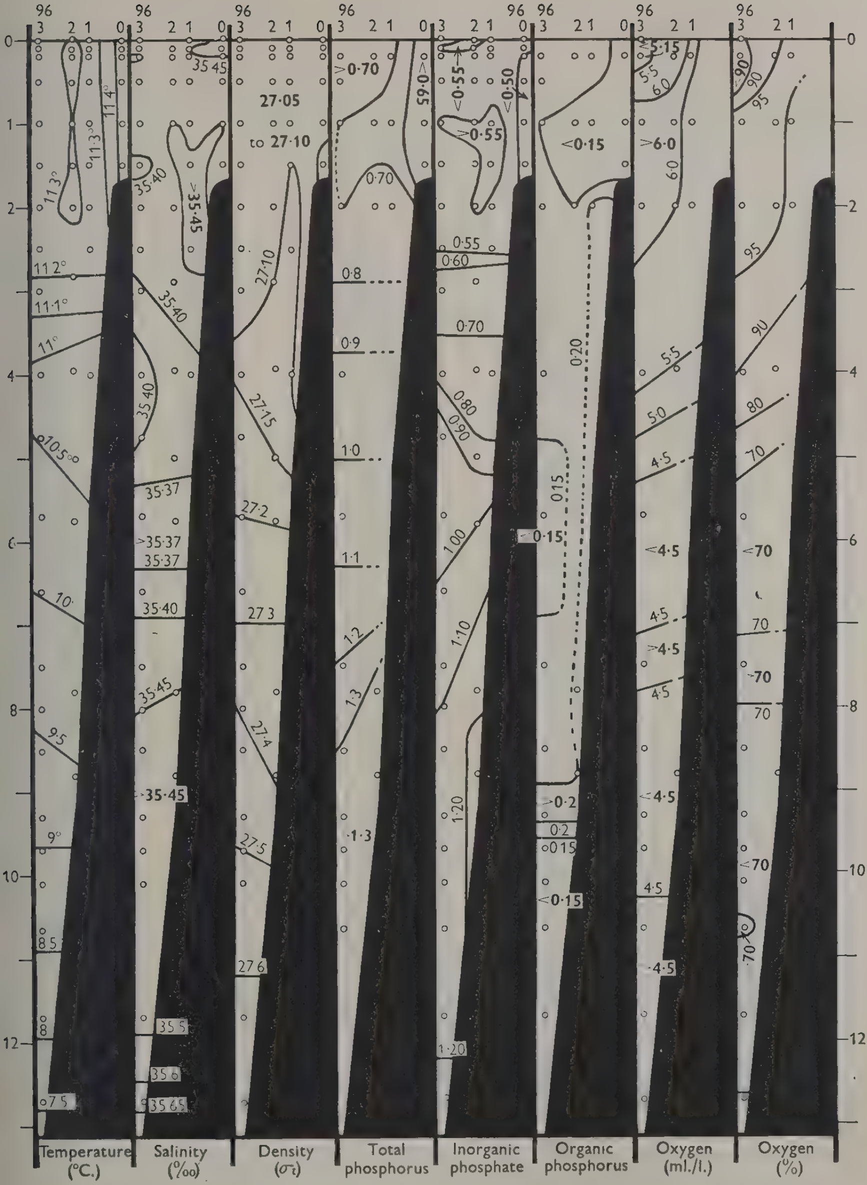

Fig. 13. Sections worked by R.R.S. *William Scoresby* on 18–19 January 1950, illustrating the distribution of properties over the continental slope west of the Celtic Sea along the parallel of latitude 50° 34′ N. Phosphorus and phosphate in μg.-atom/l. P. Depths in hundreds of metres.

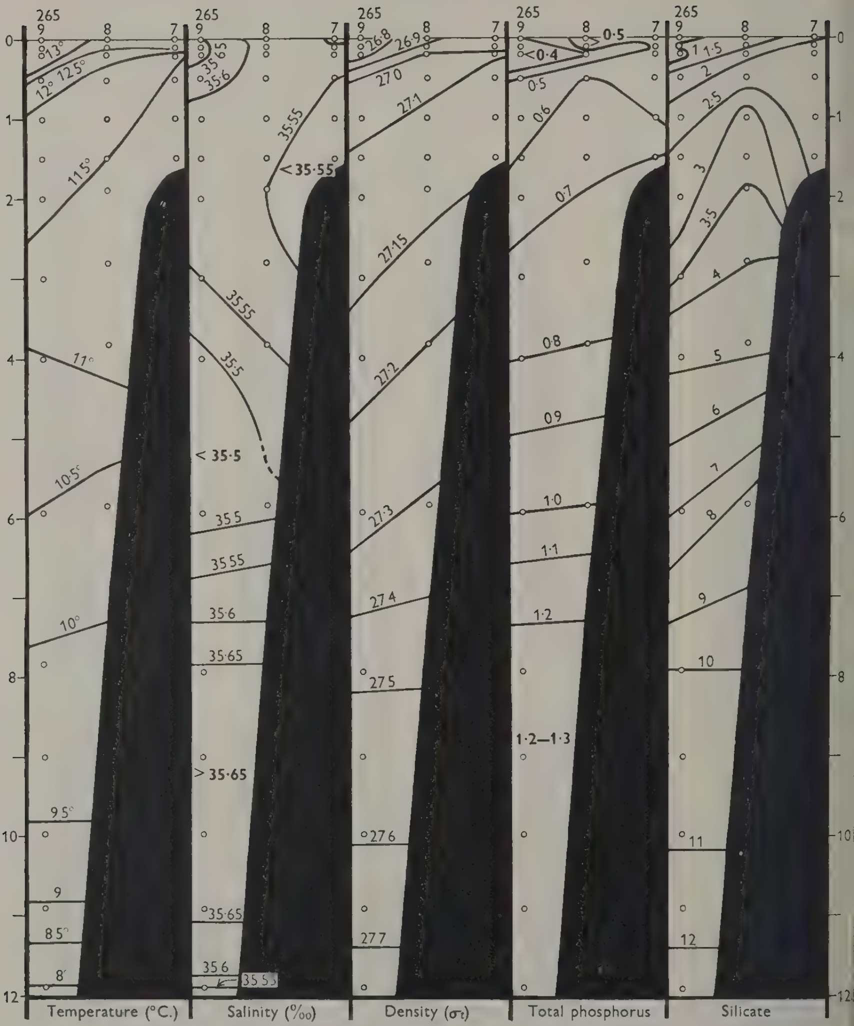

Fig. 14. Sections worked by R.R.S. *Discovery II* on 11–12 May 1950, illustrating distribution of properties over the continental slope south of the Celtic Sea approximately along the meridian 7° 40′ W. Phosphorus and silicate in μg.-atom/l. Depths in hundreds of metres.

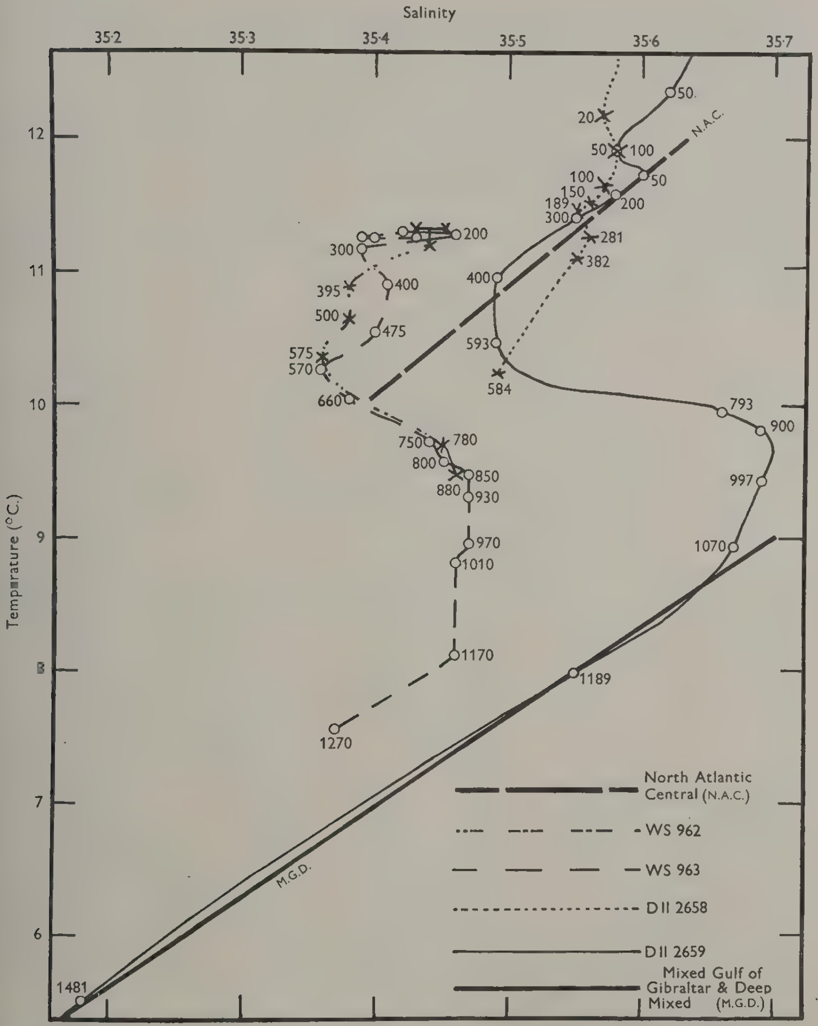

Fig. 15. Temperature-salinity relationships for the two *William Scoresby* stations (962, 963) and the two *Discovery II* stations (2658, 2659) over the continental slopes of the Celtic Sea in 1950.

### *The Deeper Waters*

On the southern section in May, the salinity maximum at around 1000 m., characteristic of the Gulf of Gibraltar water, was well developed (Fig. 14, panel 2). It was also recognizable on the northern section in January. It had the properties set out in Table XI.

Determinations of silicate, in addition to those of oxygen, are likely to assist in distinguishing deep cascaded water from Gulf of Gibraltar water. Silicate determinations are also likely to distinguish cascaded from capsized water.

Above the Gulf of Gibraltar water lay water of minimum salinity and having the properties set out in Table XII.

TABLE XI. PROPERTIES OF THE GULF OF GIBRALTAR WATER IN THE EARLY MONTHS OF 1950

| | | | |
|---|---|---|---|
| Salinity | 35·6 ‰ | Total phosphorus | 1·2– 1·3 μg.-atom/l. |
| Temperature | 8·9 –10·0° C. | Phosphate phosphorus | 1·1– 1·2 μg.-atom/l. |
| $\sigma_t$ | 27·45–27·68 | Silicate-Si | 10 –11·5 μg.-atom/l. |

TABLE XII. PROPERTIES OF MINIMUM SALINITY WATER

| | | | |
|---|---|---|---|
| Salinity | 35·49 ‰ | Total phosphorus | 0·6–1·0 μg.-atom/l. |
| Temperature | 10·25–10·95° C. | Silicate-Si | 4·8–8·3 μg.-atom/l. |
| $\sigma_t$ | 27·18–27·32 | | |

TABLE XIII. SOME PREDICTED PROPERTIES OF THE SEVERAL TYPES OF WATER MASS FOUND NEAR THE CONTINENTAL SLOPE OF THE CELTIC SEA

| | Oxygen (%) | Silicate-Si (μg.-atom/l.) | Total phosphorus (μg.-atom/l.) | Temperature (°C.) | Salinity (‰) |
|---|---|---|---|---|---|
| Cascaded water | >85 | <4 | <0·7 | Uniform and dependent on origin | Uniform and dependent on origin |
| Capsized water | High and uniform | *c.* 6 | *c.* 0·9 | Uniform and > 10 | Uniform and > 35·5 |
| Gulf of Gibraltar water | 65–69 | 10–11·5 | 1·2–1·3 | 9·0 ± 0·5 | Maximal and > 35·5 |
| Deeper North Atlantic Central water | 65–70 | > 10 | > 1·3 | Conforming to standard *T–S* diagram | Conforming to standard *T–S* diagram |

The rapid increase in nutrient content through the layer of minimum salinity is very striking.

The low-salinity component of this water can come neither from above nor below. It can arise only by lateral mixing. Two origins are possible, either North Atlantic Central water from much the same depth to the south-west, or cascaded water directly from the Porcupine Bank or round by the South Porcupine submarine promontory from the Hebridean continental shelf. At *William Scoresby* station 963 on 19 January 1950 the low oxygen content

(63·5 % saturated) at the salinity minimum at 575 m. indicates surely that then North Atlantic Central water was dominant there.

The predicted properties set out in Table XIII will certainly be modified in detail by further knowledge. They are meant to show how, by combining several determinations, it should become possible in this area to recognize with certainty the several water masses and admixtures of them.

### The Hydrography of the Submarine Indentation South of the Porcupine Bank and South-west of County Kerry

On twenty-seven occasions the Irish Fisheries Service, under the direction of the late Mr G. P. Farran, has made observations at the station SS (50° 34′ N., 11° 17′ W. approximately) on the eastern side of the submarine indentation (Table XIV). The results for the years 1910–14 have been read from Mr D. J. Matthews's record cards, now in the writer's possession, and those for later years have been extracted from the *Bulletins Atlantiques* and *Bulletins Hydrographiques* published by the International Council for the Exploration of the

TABLE XIV. OBSERVATIONS AT THE IRISH STATION SS, 50° 34′ N., 11° 17′ W. APPROXIMATELY

| Station no. | Lat. 50° N.+ | Long. 11° W.+ | Date | Depth to bottom (m.) | Depth of samples taken below 601 m. |
|---|---|---|---|---|---|
| SR 992 | 34′ | 29′ | 9. viii. 10 | 1452 | 713, 1225 |
| SR 1098 | 37½′ | 16′ | 11/12. ii. 11 | 1006 | 700, 956 |
| SR 1158 | 33′ | 21′ | 15. v. 11 | 1234–1478 | 731, 1234 |
| SR 1228 | 36′ | 19′ | 10. viii. 11 | 1167 | 823, 1097 |
| SR 1379 | 31′ | 16′ | 11. v. 12 | 977 | 731, 914 |
| SR 1439 | 27′ | 20′ | 14. viii. 12 | 951 | 640, 914 |
| SR 1613 | 29′ | 22′ | 15. v. 13 | 960 | 640, 914 |
| SR 1677 | 35′ | 18′ | 14. viii. 13 | 1072 | 731, 987 |
| SR 1824 | 33′ | 23′ | 14. v. 14 | 1379 | 914, 1280 |
| SR 2158 | 34′ | 17′ | 14. v. 25 | 1037 | 1000 |
| SR 2173 | 34′ | 17′ | 24. xi. 25 | 1152 | 1097 |
| SR 2221 | 34′ | 17′ | 17. viii. 26 | 797 | 768 |
| SR 2244 | 34′ | 17′ | 19. ii. 27 | 906 | 860 |
| SR 2270 | 34′ | 17′ | 10. v. 27 | 1004 | 966 |
| SR 2290 | 34′ | 17′ | 27. xi. 27 | 1049 | 1024 |
| SR 2311 | 34′ | 16′ | 14. iv. 28 | 906 | 878 |
| SR 2353 | 34′ | 16′ | 21. ii. 29 | 1016 | 986 |
| SR 2382 | 35′ | 12′ | 3. vi. 29 | 843 | 800 |
| SR 2404 | 36′ | 15′ | 12. viii. 29 | 873 | 840 |
| SR 2420 | 34′ | 16′ | 1. xii. 29 | 1027 | 750, 978 |
| SR 2487 | 37′ | 19′ | 26. v. 31 | 856 | 695 |
| SR 2509 | 34′ | 14′ | 17. viii. 31 | 767 | 750 |
| SR 2533 | 38′ | 14′ | 3. ii. 32 | 769 | 720 |
| *Challenger* 1 | 25′ | 15′ | 26. vi. 32 | 815 | 750, 795 |
| SR 2585 | 41′ | 17′ | 8. viii. 32 | 989 | 700, 800, 950 |
| SR 2648 | 35′ | 16′ | 17. v. 33 | 1016 | 700, 800, 969 |
| SR 2664 | 35′ | 16′ | 8. viii. 33 | 1073 | 700, 800, 1042 |
| SR 2725 | 34′ | 15′ | 12. vi. 34 | 847 | 700, 800 |
| WS 962 | 34′ | 10′ | 18. i. 50 | 922 | 780, 880 |
| WS 963 | 34′ | 30′ | 19. i. 50 | 1311 | 660, 750, 800, 850, 930, 970, 1010, 1065, 1170, 1270 |

Sea. The series has been supplemented by one by H.M.S. *Challenger* in 1932 (Cons. Int., *Bull. Hydrogr.* for 1932) and by interpolated results from the two outermost *William Scoresby* stations in 1950 (Cons. Int., *Bull. Hydrogr.* for 1950). Depths observed ranged from 767 to 1478 m.

Mean temperatures, salinities and densities have been evaluated (Table XV), by interpolation where necessary, for standard depths at intervals of 100 m. from 100 to 1000 m. Down to 600 m., the sampling intervals were small enough to make interpolation safe except on 17 August 1931. Below 601 m. in many years only one depth was sampled so that interpolation may have caused error. The curves have been slightly adjusted so that salinity, temperature and density are consistent. Moreover, on some occasions, bottom was found above 800 m. Although the assessment of mean values at 800–1000 m. must be subject to greater error than in the upper waters, the error of the temperature mean appears not to exceed ±0·02° C. Standard deviations of the means are also included in Table XV.

TABLE XV. MEAN TEMPERATURES, SALINITIES AND DENSITIES AT STANDARD DEPTHS AT OR NEAR THE IRISH STATION SS (50° 34′ N., 11° 17′ W.) FOR TWENTY-NINE OCCASIONS, WITH STANDARD DEVIATIONS

| Depth (m.) | Temperature (° C.) | Salinity (‰) | Density ($\sigma_t$) |
|---|---|---|---|
| 100 | 11·02 ± 0·43 | 35·52 ± 0·04$_9$ | 27·19 ± 0·08$_2$ |
| 200 | 10·74 ± 0·26 | 35·52 ± 0·06$_2$ | 27·24 ± 0·05$_0$ |
| 300 | 10·62 ± 0·22 | 35·52 ± 0·05$_1$ | 27·26 ± 0·03$_6$ |
| 400 | 10·50 ± 0·19 | 35·51 ± 0·06$_0$ | 27·28 ± 0·03$_5$ |
| 500 | 10·31 ± 0·14 | 35·50 ± 0·04$_4$ | 27·30 ± 0·03$_8$ |
| 600 | 10·09 ± 0·14 | 35·50 ± 0·05$_5$ | 27·34 ± 0·04$_7$ |
| 700 | 9·83 ± 0·20 | 35·51 ± 0·04$_5$ | 27·40 ± 0·04$_5$ |
| 800 | 9·54 ± 0·27 | 35·54 ± 0·04$_0$ | 27·47 ± 0·04$_8$ |
| 900 | 9·28 ± 0·31 | 35·55 ± 0·04$_5$ | 27·52 ± 0·05$_0$ |
| 1000 | 8·92 ± 0·43 | 35·54 ± 0·04 | 27·57 ± 0·06$_2$ |

Vertical mixing would seem to proceed at all depths on a considerable scale (Cooper, 1952*a*, fig. 2). Although the water at 1000 m. is commonly of very different origin from that at 100 m., the uniformity in salinity from top to bottom is notable. The result illustrates the futility of treating all high-salinity waters in the Celtic Sea as carrying uniform chemical and biological properties.

The stratum of most constant temperature lies between 500 and 600 m., that of most constant density between 300 and 500 m. The deepest water at 1000 m. shows a greater range of temperature and of density than any other stratum below 150 m. A similar result has been found in the open Atlantic at 44° 36′ N., 20° 00′ W. (Fig. 2). The relatively large standard deviation of the density at 1000 m. must mean that the currents there are of the same order of magnitude as those at 100 m. These deep currents will affect all attempts at dynamic computation of surface currents. The reference level of assumed no motion in the Eastern North Atlantic needs to be taken very deep. Moreover, the strong slope of deep geopotential topographies should have a very pronounced effect, possibly a controlling effect, on surface currents. It may explain, in part, the great difficulty in assessing surface currents in the Atlantic near the continental slope of the Celtic Sea.

### *Variations in the Gulf of Gibraltar and 'Rockall Cascade' Waters at Station SS*

The strength of the tongue of Gulf of Gibraltar water varies much from time to time. The largest changes between successive observations are given in Table XVI. Between May and August 1911 water entered between 700 and at least 820 m. depth which was both much warmer and more saline; it was undoubtedly Gulf of Gibraltar water. Between the same months in 1933, the converse happened, the Gulf of Gibraltar water was pushed out by colder and less saline water. This is the more usual occurrence.

TABLE XVI

| | Increase in salinity (‰) | | | Increase in temperature (° C.) | | |
|---|---|---|---|---|---|---|
| Dates | 800 m. | 900 m. | 1000 m. | 800 m. | 900 m. | 1000 m. |
| (*a*) Salinity and temperature increased or decreased together | | | | | | |
| 15. v.–10. viii. 11 | +0·09 | — | — | +0·63 | +0·69 | +0·70 |
| 17. v.–8. viii. 33 | −0·07 | −0·09 | −0·09 | −0·30 | −0·40 | −0·52 |
| (*b*) Salinity and temperature moved in opposite phase | | | | | | |
| 27. xi. 27–14. iv. 28 | +0·06 | +0·08 | — | −0·62 | −0·78 | — |
| 14. viii. 12–13. v. 13 | −0·06 | −0·06 | — | +0·23 | +0·21 | — |

During the winter of 1927–8 between November and April at about 880 m. water about 0·08 ‰ more saline but half a degree colder came in; yet in the winter of 1912–13 at about 900 m. water 0·06 ‰ less saline and 0·20° C. warmer entered. These last events cannot be correlated with changes in the Gulf of Gibraltar component. A detailed study of variations in salinity on the lines of the analysis of temperature to follow has not revealed any rhythmic change in the distribution of salinity.

There are striking variations in temperature at 800–1000 m. depth, but owing to the heterogeneous nature of the data they are not presentable in a simple form. They may be most surely shown by the following procedure. (i) The temperatures at 100 m. intervals from 100 to 1000 m. were tabulated, when necessary interpolating graphically and checking that temperatures, salinity and density are mutually consistent. (ii) The mean temperature at each standard depth for all observations at station SS was then evaluated. (iii) At 800, at 900 and at 1000 m., the deviations of each observed or interpolated temperature from the mean for the depth was worked out. (iv) The deviations at 800 m. and, when available, at 900 and 1000 m., were then averaged to give the best assessment possible of the mean deviation of the temperature of the 800–1000 m. stratum from its overall average. (v) The changes in these mean deviations as measured on cruises a quarter or half year apart were then computed (Table XVII).

The result is no more than a measure of the changes in the temperature of the 800–1000 m. stratum considered as a whole. The summer of 1911 was exceptional (p. 495), and all results involving it are enclosed in square brackets and omitted from the means.

There is a seasonal change in temperature with a range of about 0·5° C. The water at 800–1000 m. has been warmest in November and coldest in August. Nearly all the warming up occurs between August and November.

TABLE XVII. CHANGES IN THE MEAN TEMPERATURE OF THE 800–1000 M. STRATUM AT STATION SS BETWEEN CRUISES A QUARTER AND A HALF-YEAR APART

Quarterly intervals

| | | | | | | | *Mean* |
|---|---|---|---|---|---|---|---|
| | 1911 | 1927 | 1929* | | | | |
| Feb.–May | [−0·48] | −0·60 | −0·17 | | | | *−0·39* |
| | 1911 | 1912 | 1913 | 1929 | 1932† | 1933 | |
| May–Aug. | [+0·68] | −0·14 | −0·04 | −0·04 | −0·22 | −0·40 | *−0·17* |
| | 1929 | | | | | | |
| Aug.–Nov. | +0·28 | | | | | | *+0·28* |
| Nov.–Feb. | No pairs of observations available | | | | | | — |

Half-yearly intervals

| | | | | *Mean* |
|---|---|---|---|---|
| | 1927/8 | | | |
| Nov.–Apr. | −0·78 | | | *−0·78* |
| | 1911 | 1929 | | |
| Feb.–Aug. | [+0·20] | −0·25 | | *−0·25* |
| | 1925 | 1927 | 1929 | |
| May–Nov. | +0·01 | +1·16 | +0·24 | *+0·47* |
| | 1910/11 | 1926/27 | | |
| Aug.–Feb. | +0·12 | +0·44 | | *+0·28* |

*Also*

| | 1910/11 | 1911/12 | 1912/13 | 1913/14 | 1926/27 | 1931/32‡ | 1932/33 | 1933/34 | *Mean* |
|---|---|---|---|---|---|---|---|---|---|
| Aug.–May | [−0·36] | [+0·23] | +0·22 | +0·08 | −0·16 | +0·42 | +0·51 | +0·31 | *+0·23* |

* 21 Feb.–3 June. † 26 June (*Challenger* Station 1)–8 Aug.
‡ 17 Aug. 1931–26 June 1932.

Analysis of the observations by other methods has shown that the extent of the cooling between May and August has been somewhat exaggerated; most of the cooling occurs between February and May, the season of cascading of shelf water (Cooper & Vaux, 1949), which undoubtedly may affect the water down to 1000 m. depth.

Water in the Celtic Sea never becomes heavy enough to sink so far and it is doubtful if Porcupine Bank water could either. Water of sufficient density could only be found at the surface still farther north. None the less, north of 60° N. and also over the Rosemary Knoll[1] the salinity is almost always too low. Over the extensive Rockall Table Mount[1] water of appropriate density, salinity and temperature often occurs. I am much indebted to Lt.-Cmdr. J. R. Lumby, R.N., for providing me from his card index with a complete set of surface hydrographical observations for the months of January to April over the Rockall Table Mount between 56° 30′ and 58° 15′ N. lat. and 13° and 15° W. long. From them the mean surface density there has been computed for each month (Table XVIII); 21 % of these observations show a surface salinity of 35·45 ‰ or more. During passage south the salinity of Rockall cascade water would be expected to increase somewhat, due to lateral mixing.

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[1] Name in accordance with the recommendations of the British National Subcommittee on Nomenclature of Ocean Bottom Features.

Considering only the statics of the system, heavy saline water formed in winter over the Rockall Table Mount could account for the fairly regular seasonal fluctuation of the water at 800–1000 m. depth at station SS (cf. also Nansen, 1912). However, the dynamics of a north-south section across the North Atlantic Drift requires a density distribution in this sense with heavy surface water on the left or north and light water on the right or south. Even so, if a cold winter produces a sudden increase in the density of the water overlying the shallow Rockall Table Mount, then the steady state of the drift would be upset. Either its speed towards the east or north-east must increase to carry a greater volume of saline water into the northern North Sea, or the heavy water must cascade towards the south, undercutting the North Atlantic Drift. Both may probably happen to different degrees in different years. Tait (1951) has remarked that in the northern North Sea the predominance of oceanic influence is in most years at a maximum in spring and early summer and at a minimum in autumn and winter, and that these seasonal variations are subject to annual fluctuations in their magnitude and incidence. This, qualitatively, is the effect which increase in density during cold weather in February and March over the shallow Rockall Table Mount and the neighbouring banks or knolls would produce. The evidence from station SS and from *Armauer Hansen* station 1914/6 is that this heavy water may also cascade and then flow southwards along the continental slope in some winters for over 500 miles.

TABLE XVIII

| Month | Mean density of surface water over Rockall Table Mount: No. of observations | $\sigma_t$ | Depth at station SS at which such a mean density is recorded; from Table XV (m.) |
|---|---|---|---|
| January | 12 | 27·46 | 790 |
| February | 12 | 27·57 | 1000 |
| March | 26 | 27·50 | 860 |
| April | 33 | 27·44 | 750 |

Although incursions of Gulf of Gibraltar water will lead to warming up at any season, it seems clear that only in the summer of 1911 was it dominant over the seasonal oscillation due to the 'Rockall cascade' current. The greatest changes in density occurred: (i) August 1910–February–May 1911 when the overall increase much exceeded 0·10 $\sigma_t$-unit; (ii) February–May 1927 when the density increased by 0·09 $\sigma_t$-unit due entirely to a fall in temperature of 0·5° C. On the latter occasion the salinity scarcely changed. The phenomenon was probably associated with cascading from the continental shelf of water having salinity 35·55 ‰, temperature 8·2–9·2° C. and density 27·54–27·68 $\sigma_t$-unit. Such water cannot have originated in the Celtic Sea and can only have come from farther north. On 1 February 1927 water having salinity 35·48 ‰, temperature 8·2° C. and $\sigma_t$ 27·65 was reported (Cons. Int., *Bull. Hydrogr.* for 1927) on the Danish line of surface stations between Copenhagen and New York at 59° 02′ N., 11° 00′ W. It is likely, therefore, that the chilled water at station SS (50° 34′ N., 11° 17′ W.) had been formed by cooling and cascading of the water in the North Atlantic Drift passing over the Rockall Table Mount. North Atlantic Central water carried towards Rockall is likely, whilst on passage around and over the Table Mount, to be modified by capsizing against the island slope during high winds. If the Rockall Table Mount was indeed its origin it had subsequently moved south at the rate of about 5 miles a day. The year 1934 showed the effect particularly clearly (Table XIX).

TABLE XIX

| Date | Lat. N. | Long. W. | Depth (m.) | Temp. (° C.) | Salinity (‰) | Density ($\sigma_t$) | Oxygen (%) |
|---|---|---|---|---|---|---|---|
| | | | Over Rockall Table Mount | | | | |
| 15. i. 34 | 58° 09′ | 14° 21′ | 0 | 8·7 | 35·40 | 27·50 | — |
| 4. ii. 34 | 57° 48′ | 13° 04′ | 0 | 9·1 | 35·46 | 27·48 | — |
| 12. iii. 34 | 58° 03′ | 13° 09′ | 0 | 8·7 | 35·52 | 27·59 | — |
| 25. iii. 34 | 58° 05′ | 13° 03′ | 0 | 9·2 | 35·48 | 27·48 | — |
| 16. iv. 34 | 57° 39′ | 13° 37′ | 0 | 9·6 | 35·59 | 27·49 | — |
| | | | Station SS | | | | |
| 12. vi. 34 | 50° 34′ | 11° 15′ | 600 | 9·81 | 35·57 | 27·45 | — |
| | | | 700 | 9·81 | 35·55 | 27·43 | — |
| | | | 800 | 9·41 | 35·57 | 27·52 | — |
| | | | Also *Armauer Hansen* station 1914/6 | | | | |
| 5. vi. 14 | 47° 57′ | 9° 42′ | 800 | 9·94 | 35·53 | 27·39 | 90 |
| | | | 1200 | 8·51 | 35·52 | 27·62 | 89 |

There is little doubt that at station SS in June 1934 there was a large northern component at 600–800 m. Similarly, the highly oxygenated waters reported from the *Armauer Hansen* expedition in 1914 by Gaarder (1927) at station 6 at 800 and 1200 m., sandwiching oxygen-depleted water (72 and 77·5 % saturated) at 900 and 1000 m., would seem certainly to have been of northern surface origin.

Ability to cascade from north to south depends not on any absolute but on relative values of density. Thus ten observations of computed surface density by Ocean Weather ships over the Rockall Table Mount in February–April 1950 revealed a somewhat low mean density of 27·41 $\sigma_t$. Nevertheless, the waters at station SS in the 'South Porcupine submarine indentation' in January 1950, also light relative to earlier years, could have subsequently accommodated such water down to 900 m. Considerable north-south cascading was possible.

The dynamics of such a descending mid-water current of cascade origin, hugging the continental slope on its left, needs attention. It is clear that immediately west of the British Isles in spring and summer geopotential topographies (for definition see Sverdrup *et al.* (1942, p. 404)), suggesting surface currents to the north and north-east, need to be interpreted with especial care. A mid-water descending current in the opposite direction and of considerable magnitude is always likely. It is now realized that such a current system would contribute to the difficulty experienced in interpreting the *Dana* section across it in June 1938. This has not been re-examined.

In March and April and even perhaps in May, severe gales from between south-west and north-west would, by causing capsizing, destroy this descending mid-water cascade current during its passage along the western fringe of the British Isles. Northern cascade water would not then reach south-west Ireland in an identifiable form.

The winter and spring of 1927 was a period of strong cascading (Cooper & Vaux, 1949). The low inorganic phosphate found that year by Atkins at 860 m. at station SS (Table X, and compare Cooper 1952*a*, fig. 2) suggests that by mid-February little water from the south was present. During the spring cascading from the Celtic Sea continued strongly, followed during the summer and autumn by a very strong recession of cascade water. By November the water at 1000 m. had warmed up by $1\frac{1}{4}$° C. and had become lighter than any water recorded there between 1910 and 1934. By April 1928 this warm light water had again been displaced by a dense, saline water of intermediate temperature (35·61 ‰, 9·0–9·4° C. and $\sigma_t$ 27·58–27·61), this water having a strong Gulf of Gibraltar component. It is clear that during 1927, as a whole, water movements around 800–1000 m. were on a scale greater than in any other year for which we have sufficient records (Table XIV). Quite apart from vertical exchanges, the resulting alterations of deep geopotential topographies must have had a very considerable effect on those at the surface. Unusual surface currents above the continental slope of the western Celtic Sea were likely in that year.

### *Seasonal Variations at Station SS in the* 200–400 *m. Water Stratum*

The seasonal variations for the 200–400 m. stratum have been worked out in the same way as those at 800–1000 m. (Table XX). The scarcity of observations in November has made difficult the distribution of changes as between autumn and early winter. Most surprising was that the changes in temperature from season to season at 200–400 m. were on an average less than one-fifth of those at 800–1000 m. The remaining conclusions are tabulated in Table XXI.

TABLE XX. CHANGES IN THE MEAN SALINITY AND TEMPERATURE OF THE 200–400 M. STRATUM AT STATION SS BETWEEN CRUISES A QUARTER OR A HALF-YEAR APART

*Salinity*

Quarterly intervals

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1911 | 1927 | 1929* | 1932 | | | | *Mean* |
| Feb.–May | +0·05 | −0·10 | +0·11 | +0·01 | | | | *+0·02* |
| | 1911 | 1912 | 1913 | 1929 | 1931 | 1932† | 1933 | |
| May–Aug. | −0·03 | −0·01 | −0·01 | −0·05 | −0·13 | −0·01 | −0·05 | *−0·04* |
| | 1929 | | | | | | | |
| Aug.–Nov. | −0·05 | | | | | | | *−0·05* |
| Nov.–Feb. | No pairs of observations available | | | | | | | — |

Half-yearly intervals

| | | | | |
|---|---|---|---|---|
| | 1927/28 | | | *Mean* |
| Nov.–Apr. | +0·04 | | | *+0·04* |
| | 1911 | 1929 | 1932 | |
| Feb.–Aug. | +0·02 | +0·06 | 0·00 | *+0·03* |
| | 1925 | 1927 | 1929 | |
| May–Nov. | −0·04 | +0·05 | −0·06 | *−0·02* |
| | 1910/11 | 1926/27 | 1931/32 | |
| Aug.–Feb. | +0·01 | +0·07 | +0·11 | *+0·06* |

*Also*

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1910/11 | 1911/12 | 1912/13 | 1913/14 | 1926/27 | 1931/32‡ | 1932/33 | 1933/34 | *Mean* |
| Aug.–May | +0·06 | 0·00 | +0·01 | −0·03 | +0·07 | +0·11 | +0·03 | +0·05 | *+0·04* |

*Temperature*

Quarterly intervals

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1911 | 1927 | 1929* | 1932 | | | | *Mean* | *Mean omitting 1932* |
| Feb.–May | −0·08 | −0·13 | −0·07 | −0·61 | | | | *−0·22* | *−0·09* |
| | 1911 | 1912 | 1913 | 1929 | 1931 | 1932† | 1933 | | |
| May–Aug. | +0·06 | +0·08 | −0·12 | +0·08 | −0·09 | +0·02 | −0·01 | *Nil* | *Nil* |
| | 1929 | | | | | | | | |
| Aug.–Nov. | +0·18 | | | | | | | *+0·18* | *+0·18* |
| Nov.–Feb. | No pairs of observations available | | | | | | | — | — |

Half-yearly intervals

| | | | | | |
|---|---|---|---|---|---|
| | 1927/28 | | | *Mean* | *Mean omitting 1932* |
| Nov.–Apr. | −0·17 | | | *−0·17* | *−0·17* |
| | 1911 | 1929 | 1932 | | |
| Feb.–Aug. | −0·02 | +0·01 | −0·59 | *−0·20* | *Nil* |
| | 1925 | 1927 | 1929 | | |
| May–Nov. | +0·13 | +0·33 | +0·26 | *+0·24* | *+0·24* |
| | 1910/11 | 1926/27 | 1931/32 | | |
| Aug.–Feb. | +0·04 | −0·03 | +0·68 | *+0·23* | *Nil* |

*Also*

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1910/11 | 1911/12 | 1912/13 | 1913/14 | 1926/27 | 1931/32‡ | 1932/33 | 1933/34 | *Mean* |
| Aug.–May | −0·04 | −0·06 | −0·03 | +0·06 | −0·16 | +0·07 | +0·12 | −0·03 | *−0·01* |

* 21 February–3 June. † 26 June (*Challenger* Station 1)–8 August.
‡ 17 August 1931–26 June 1932.

TABLE XXI. SEASONAL VARIATIONS AT STATION SS IN THE 200–400 M. WATER STRATUM

| | Temperature | Salinity |
|---|---|---|
| Feb.–May | Average decrease of at least 0·09° C. Very marked decrease (0·6°) in 1932 | Variable. Average increase of merely 0·02 ‰. In 1927, a year of strong cascading of shelf water, there was a decrease of 0·10 ‰. For 1930, probably a year of strong cascading, no observations are available |
| May–Aug. | Little change | Decrease in every year, average decrease 0·04 ± (S.D.) 0·04 ‰. (The statistical distribution is not 'normal'.) |
| May–Nov. | Average increase of 0·2°, mostly between August and November | Little regular change |
| Aug.–Feb. | Net slight overall tendency to increase; very strong warming (0·7°) in autumn of 1931–32 | Average increase of about 0·06 ‰ |

N.B. Owing to the nature of the distribution of the observations in time, the positive and negative assessments cannot be expected exactly to cancel.

| | Density |
|---|---|
| Feb.–May | Average increase of about 0·06 $\sigma_t$-unit |
| May–Aug. | Average decrease of about 0·03 $\sigma_t$-unit |
| Aug.–Nov. | Average decrease of about 0·03 $\sigma_t$-unit |
| Nov.–Feb. | Little change |

### *Recent Warming up of the Upper layers at Station SS*

For the twenty-nine sets of observations at and near station SS the departures from the mean temperature of the 200–400 m. stratum are presented in Table XXII. Positive departures are stressed by italic type. In the years 1910–14 and again from May 1925 to May 1927 the water was consistently colder than the average by 0·2° C. No records are available for the exceptionally warm autumn of 1921 (cf. Harvey, 1923).

During the summer of 1927 markedly warmer water arrived and remained with minor recessions until the end of the Irish observations in 1934.

When the position was next examined on 18–19 January 1950 by R.R.S. *William Scoresby*, the stratum was found to be 0·7° C. warmer as compared with 1910–14 and 1925 (cf. Helland-Hansen, 1949).

Smed (1949*a*,*b*, 1950) has found that there has been a warming up since about 1932 of the surface waters in the north-eastern North Atlantic in his areas I, H and L (between 55 and 67° N. lat. and between 10 and 20° W. long.), in area J (between 60 and 64° N. and between 0 and 10° W.), and in area K (between 58 and 60° N. and between 3 and 10° W.). It would seem from his reports that the marked warming up first appeared in the north about 1927 and that it is spreading towards the south and south-west. His findings seem to be compatible not with an increased transport of heat by the North Atlantic Drift but rather with reduced abstraction in the north of the heat transported. If this has been so, winter cascading from the more northern shallow areas, such as the Rockall Table Mount, will have been affected and the rate of formation of the North Atlantic Deep water still farther north may have been reduced (see also Cooper, 1952*b*).

On the other side of the Atlantic, Lauzier (1950) has reported that from April to October 1949 the surface temperatures at St Andrews (mouth of the Bay of Fundy) and at Halifax (Nova Scotia) Lightvessel were much higher than usual, indeed the highest ever recorded.

TABLE XXII. WARMING UP OF UPPER WATERS (200–400 M.) AT STATION SS BETWEEN 1910 AND 1950, SHOWN BY DEPARTURES FROM MEAN TEMPERATURES

(Positive departures in italic type.)

| Year | February | May | August | November | Period average |
|---|---|---|---|---|---|
| 1910 | — | — | −0·20 | — | |
| 1911 | −0·16 | −0·24 | −0·18 | — | |
| 1912 | — | −0·24 | −0·16 | — | |
| 1913 | — | −0·19 | −0·31 | — | |
| 1914 | — | −0·25 | — | — | |
| Mean 1910–14 | −0·16 | −0·23 | −0·21 | — | −0·18 |
| 1924 | — | −0·30 | — | −0·17 | |
| 1926 | — | — | 0·00 | — | |
| 1927 | −0·03 | −0·16 | — | — | |
| Mean 1925–May 1927 | — | — | — | — | −0·13 |
| 1927 | — | — | — | *+0·17* | |
| 1928 | — | 0·00 | — | — | |
| 1929 | *+0·20* | *+0·13* | *+0·11* | *+0·39* | |
| 1930 | — | — | — | — | |
| 1931 | — | *+0·02* | −0·07 | — | |
| 1932 | *+0·48* | *+0·04* | *+0·02* | — | |
| 1933 | — | *+0·14* | *+0·13* | — | |
| 1934 | — | *+0·10* | — | — | |
| Mean November 1927–May 1934 | *+0·34* | *+0·07* | *+0·08* | *+0·28* | *+0·19* |
| 1950 | *+0·52*<br>(January) | — | — | — | (*+0·52*) |

These events reflect the general warming up of the North Atlantic. One result is that the temperature-salinity relationships, epitomized in equations (1) and (2) (pp. 467 and 479) and drawn in Figs. 9 and 15, now refer to an age that is past. They need to be re-determined from fresh observations.

## DISCUSSION

The purpose of this paper has been twofold: first, by achieving a better understanding of the exchanges of water with the Atlantic, to assist the preparation of papers to follow on the hydrography of the Celtic Sea and English Channel; and, secondly, to enable future investigations over the continental slope to be better directed to the solution of defined problems. It is a contribution to 'experimental oceanography'.

There is clearly a need for repeated observations at fixed points in deep water off the slope to keep track of the very considerable fluctuations which occur at all depths above 1500 m.

The theory of 'capsizing' water masses over the continental slope seems plausible. If capsizing can be shown to be dynamically sound and can be demonstrated by clear-cut observations, it provides a mechanism of great power for enriching the surface waters of the sea with deep nutrients.

It seems probable that, in general terms, winds of a given strength will prove very much more effective in producing extensive capsizing if preceding conditions have been optimal. Many variations of circumstances can be visualized. Thus, if strong winds have blown from between north and east for some time, as they did in February 1947, some degree of upwelling by the classical mechanism would occur. If then the wind veered quickly to the south, reaching gale force and producing severe capsizing while nutrient-rich water stood banked high against the slope, there would arise very favourable conditions for surface enrichment of a kind which would occur only a few times in a century.

It is necessary also to follow the conflict at 800–1000 m. depth between Gulf of Gibraltar water and cascade water from the north and to learn more of their properties. The Irish station SS, already worked twenty-seven times, is an obvious choice. It lies on the edge of the 'South Porcupine submarine indentation' which may act like an electrical choke, ironing out short-period fluctuations appearing in the water outside the indentation. On occasion, as on 14 May 1925 and 19 February 1927 (Cooper, 1952*a*, fig. 2), the compression of the temperature-salinity diagram suggests that vertical exchanges may become very large (cf. Atkins's determination (Table X) of inorganic phosphate at 860 m. at station SS on 19 February 1927, which was surprisingly low for such a depth). For purposes of comparison the $T$–$S$ relationship found immediately south of the Celtic Sea at *Armauer Hansen* station 1914/6 (Figs. 8 and 9) and at *Armauer Hansen* station 1914/15 in the open Atlantic are included.

In such a submarine indentation, internal waves probably resonate strongly, causing great turbulence and vertical mixing and, by so doing, destroying themselves. Combined studies of cascading, capsizing, internal waves and resonance in this indentation will be necessary. Capsizing against either wall of the indentation should itself induce deep internal waves which would be expected to resonate strongly.

An additional Irish station has been worked three times, at 50° 00′ N., 13° 00′ W. The observations there have been consistent with those at station SS. It is in a strategic position north of the 'Sole submarine promontory' which seems sometimes to be a water parting.

Cascaded shelf-waters play an important part. It will be necessary to substantiate that the deeper cascade waters, do, in fact, come from the north, probably from the Rockall Table Mount. A solution will require (i) a knowledge of the frequency of occurrence over the Rockall Table Mount, and over the other elevations of the sea-bed towards the east and north-east, of suitable water sufficiently heavy and in sufficient amount to cascade to the south and to undercut the main North Atlantic Drift; (ii) establishment of a descending current in late spring and summer along the continental slope west of the British Isles; (iii) determination of oxygen contents throughout the whole area, since waters from the Gulf of Gibraltar and the Atlantic to the south-west at around 1000 m. would be expected to have an oxygen content between 65 and 70 % saturated, whereas recently cascaded water should exceed 85 % saturated; (iv) a study of silicate distribution, which is likely to help; (v) a satisfactory account of the dynamics of a mid-water current gliding downhill towards the south with the continental slope on its left.

Cascading and capsizing are very different processes which may produce in our waters markedly similar distributions of salinity, temperature and oxygen. Often they may combine to give a large mass of water of composite origin. They should be distinguishable and the degree of admixture of the two waters or processes should be assessable in terms of the content of nutrients, especially silicate. Capsized water should be the richer.

Fraser (1950) states that the Scottish fisheries research vessels have found biological indications of two water masses approaching Faeroe from the south-west. One, the 'Lusitanian' stream, has travelled via the west coasts of Ireland and Scotland and will have been influenced by any vertical exchanges over and along the continental slope; the other, the Atlantic stream, travels farther west. The two streams, at least in the middle and late summer, are said to be very distinct but mix along the line of meeting. Such biological distinctions probably indicate chemical differences in the waters which may persist awhile. It would be desirable to know which of these waters bathes the Rockall Table Mount and other areas of formation in winter of cascaded water.

May one ask whether the 'Lusitanian' water may be identifiable with a 'capsized and cascaded water' similar to that at stations 6–8 of Fig. 11? Such water should exist all along the west European continental slope and for 75–150 miles to seaward. The 'Atlantic' water of the Scottish workers would then be identifiable with the 'North Atlantic Central' water of stations 9–15 and its winter-mixed surface skin.

The North Atlantic Drift carries warm-water plankton organisms ever northwards and eastwards into colder regions unsuitable for their reproduction. Any mechanism for returning part of the stock to the south should assist its survival. If therefore there are any organisms, not only animals but perhaps diatoms as resting spores, which can avail themselves of the deeper return current of cascade origin, their survival should be favoured. Diatom resting spores could only profit if they complete their travels by being brought up to illuminated surface waters by some form of upwelling such as capsizing. Cascade water, formed as it is in winter, will start by being reasonably rich in nutrients and will become further enriched by lateral exchange or capsizing with richer deep North Atlantic Central or Gulf of Gibraltar water. Resting spores brought up in such water to illuminated levels would be able immediately to initiate rapid cell division. In their new home they would be considered to be more northern species. If this cyclical process can be firmly established as occurring it provides not only the nutrients required for growth but the seeds of life itself.

The mid-water cascade current will take time on its journey south. It will sink in the north mostly in February and March and will not reach its southern limit until late in the spring. Species of plants and animals which may be said to be characteristic of the waters around 58–60° N., 12–15° W., and would there start their seasonal reproductive cycle in, say, March, would not reach more southern waters until later in the spring.

Again, since the intensity of cascading will be related to air and sea temperatures in the more northern area, after warm 'northern' winters the 'seed' stock of northern species of phyto- and zooplankton abreast of the Celtic Sea should be poor, while after cold 'northern' winters it should be relatively rich. It should therefore be worth while to seek a correlation between abundance of 'more northern' species in May and June between 48 and 50° N. with air and sea temperatures in February and March between 58 and 60° N. Intensity of cascading should not be related so much to deviations of temperature from all-time means but to deviations from short-period average conditions. Therefore, such a correlation should be sought not in terms of all-time but in terms of immediately preceding decade means.

South of the Celtic Sea only one position has ever been exactly repeated, viz. 46° 28′ N. lat., 8° 01′ W. long. (*Dana* stations 1387 on 25 June 1922, and 4158 on 17 June 1930). Choice of standard stations will not be much restricted by history but will depend much more upon the position of submarine valleys and spurs in the neighbouring continental slope.

## SUMMARY

The properties of 'Mediterranean' water reaching the threshold of the Celtic Sea are outlined. This water may be recognized not only by its relatively high temperature and salinity but by an oxygen content between 65 and 69% saturated. The name 'Gulf of Gibraltar' water is preferred.

Due to admixture of nutrient-rich North Atlantic Central water, the Gulf of Gibraltar water in the neighbourhood of the Celtic Sea is fairly rich in nutrients, and the large 'anomaly of the nitrate-N–phosphate-P ratio found in its region of origin has largely disappeared.

The extension of the Gulf of Gibraltar water into the eastern North Atlantic

is very variable both in space and time and, at a given position, very large changes in temperature and salinity may occur in a few months.

The *Thor* investigations in 1906 revealed that the Gulf of Gibraltar water may be held into the right against the continental slope of the west European coast and not extend very far to seaward. Between 1000 and 2000 m. depth south of the Celtic Sea variations in phosphate-P content of at least 0·2 $\mu$g.-atom/l. seem to have occurred.

The properties and upper and lower limits of North Atlantic Central water in the area have been examined. Well away from the continental slope the upper limit of Central water, conforming to its *T–S* relation, and the lower limit of winter mixing have lain between 75 and 100 m. depth. Approaching the slope the apparent depth of vertical mixing becomes more than twice as great. This effect is attributed to cooled cascade water from the continental shelf which, by bringing about a state of labile equilibrium, assists mixing to a greater depth by wind and by processes such as capsizing of water masses peculiar to the continental slope.

Part of a survey of a section of the continental slope by H.M. surveying ship *Dalrymple* revealing a rugged topography is reproduced (Fig. 10).

It is possible to identify the several water masses in the vertical section worked south-west of the Celtic Sea in June 1914 by the Norwegian research vessel *Armauer Hansen* (Fig. 11), viz. (i) North Atlantic Deep water below approximately 2000 m.; (ii) between 1200 and 2000 m. water formed by mixing of Deep water and Gulf of Gibraltar water and conforming well to the *T–S* relation given as equation (1); (iii) between 800 and 1200 m. depth Gulf of Gibraltar water showing a salinity maximum and oxygen minimum, and warm; (iv) North Atlantic Central water conforming to equation (2), 700 m. thick at *Armauer Hansen* station 15 (Figs. 8 and 9) and thinning out towards the shelf which it did not reach; (v) an intermediate region of mixed Central and Gibraltar water; (vi–viii) three layers of cascaded waters lying against the continental slope, the uppermost one extending from the surface down to 400 m. depth and derived largely from the Celtic Sea and further mixed by capsizing processes, and two others at about 800 and at 1200 m. depth of northern origin: the Porcupine Bank and the Rockall Table Mount are tentatively suggested as the sources of these; and lastly (ix) at stations 10 and 11, 200 miles off the continental slope, a core of highly oxygenated water (86–94% saturated) and having temperature and salinity appropriate to the Celtic sea the preceding winter. This core is considered to be a cascade phenomenon whose understanding demands further knowledge of the topography and oceanography of the continental slope.

It is considered probable that these water masses of very different physical and biological histories will have acquired different contents of chemical micro-constituents. These may affect organisms for good or ill at sensitive stages in their life histories, e.g. development of diatom-resting spores, fertilization and hatching of eggs and moulting of crustaceans. When 'Atlantic' water enters the Celtic Sea and English Channel, the particular kind needs to be identified.

On 18–19 January, 1950, R.R.S. *William Scoresby* worked four stations over the western continental slope of the Celtic Sea along the parallel 50° 34′ N. and on 11–12 May, R.R.S. *Discovery II* worked three over the southern slope in about 7° 40′ W. (Fig. 8). At no depth were the two sections closely related.

On the northern January section vertical mixing had extended to 250 m. and there was little horizontal difference in temperature or density. Total phosphorus and inorganic phosphate increased westward by 0·1 $\mu$g.-atom/l. in 30 miles. Along the southern section in May there was no relict isothermal, isopycnal layer from the winter.

The twenty-seven sets of observations made by the Irish Fisheries Service at their position 'SS', 50° 34′ N., 11° 17′ W., have been submitted to statistical examination. Mean temperatures, salinities and densities are set out in Table XV, together with standard deviations. The water there at 800–1000 m. depth and also at similar depths in the open Atlantic at 44° 36′ N., 20° 00′ W. shows a greater standard deviation and range of temperature and density than any other strata below 150 m. Currents there must be of the same order of magnitude as at 100 m. depth.

The conflict south-west of Ireland between Gulf of Gibraltar water and cascaded waters from the north is described. It is suggested, but not proved, that much of the northern cascaded water has been created over the Rockall Table Mount and flows south at about 5 miles a day. At station SS there is at 800–1000 m. depth a seasonal change in temperature with a range of about 0·5° C.

Immediately west of the British Isles in spring and summer geopotential topographies, derived from the distribution of density, suggesting surface currents to the north and north-east need to be interpreted with especial care. A mid-water descending current in the opposite direction and of considerable magnitude is always likely. The effect upon the survival of diatoms and of animal plankton of a cyclical process involving this mid-water return current is examined.

During 1927 as a whole, water movements around 800–1000 m. were on a scale larger than in any other year for which we have sufficient records.

At 200–400 m. depth the average seasonal changes in temperature were only one-fifth of those at 800–1000 m. Since 1927 the stratum of water between 200 and 400 m. has become warmer. In January 1950 it was 0·5° C. warmer than the mean of all observations. The relevance of these results to the widely held view that the Northern Hemisphere is warming up is discussed.

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## APPENDIX

### METHODS USED IN THE 1950 INVESTIGATIONS

The Nansen-Pettersson insulating water-bottle was used down to 400 m. at R.R.S. *William Scoresby* stations on 18–19 January and R.R.S. *Discovery II* stations on 11–12 May 1950, except at station WS962 (to 200 m.) and *Discovery II* station 2658 (to 150 m.). *Discovery* pattern reversing bottles were used at greater depths. All temperatures are appropriately corrected to give temperatures *in situ*. All salinities were determined by the Government Chemist.

The analyses of oxygen samples collected on R.R.S. *William Scoresby* were completed by Dr T. J. Hart and Mr R. I. Currie on 26 January in the ship's laboratory whilst lying at Devonport. Analyses of inorganic phosphate were made by the present Plymouth procedure (Harvey, 1948) by Mr F. A. J. Armstrong between 21 and 23 January. Total phosphorus analyses were made on 24 January by him using Harvey's method.

All R.R.S. *Discovery II* samples were taken on to Malta whence they were sent back by sea. Unfortunately, they were delayed in transit and did not arrive at Plymouth until the end of July. The samples in glass bottles for analysis of salinity by the Government Chemist and in polythene bottles for silicate analyses by Armstrong's own method (1951) were in good condition. Analyses of the inorganic phosphate samples, preserved though they had been, were not attempted. Since the samples for total phosphorus analysis in baited polythene bottles had evidently stood upside down for some time and the accuracy which may be read into them has proved of much importance, it becomes necessary to quote Mr Armstrong's detailed comments on his analyses:

> The volume of each sample was measured before autoclaving. It should have been 69 ml. (67 ml. of sea water + 2 ml. reagents). In every case it was less. After autoclaving the volume was adjusted to 68 ml. by adding distilled water and the analysis completed.
>
> Fifty of the 59 samples showed deficiencies in volume of 2–8 ml., 8 of 9–14 ml. and one (Station 2655, 10 m.) of 25 ml. Deficient volume was assumed to be the result of evaporation or spillage and it seemed likely that both had occurred. Leakage of salt water from some bottles was evident because incrusted salt was seen around the stoppers and on the underside of the lid of the box. Loss by evaporation alone would not matter since it would be made up after autoclaving, during which evaporation occurs anyway.
>
> If the samples were homogeneous, spillage could be allowed for in calculation. The variable salinity of the samples, which might be expected to introduce small and variable 'salt errors' into the analyses, does not matter since salt errors are compensated by the 'subsequent addition of phosphate' technique of Harvey (1948, p. 351). Loss of sample can be allowed for by multiplying the first result found by the ratio unspilt volume/volume found, where 'unspilt volume' is the original volume of 69 ml. less that volume lost by evaporation. Since it was impracticable to find out what proportion of the losses in each sample was due to evaporation, it was assumed arbitrarily that each sample had lost 2 ml. in this way, and the unspilt volume was taken to be 67 ml.
>
> However, the samples were not homogeneous, since they contained a $Th(CO_3)_2$ suspension likely to occlude or adsorb phosphorus so that another unknown error, difficult to estimate, is involved. The results have therefore been given to the nearest 0·1 $\mu$g.-atom/l. The true value of a result reported as, say, 0·7 is believed to lie between 0·65 and 0·75.

# FACTORS AFFECTING THE DISTRIBUTION OF SILICATE IN THE NORTH ATLANTIC OCEAN AND THE FORMATION OF NORTH ATLANTIC DEEP WATER

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(Text-figs. 1–2)

In the deep water of the eastern North Atlantic below 2000 m. the variations with depth of salinity, temperature, density, oxygen, phosphorus compounds and nitrate are quite small. By contrast the silicate content is doubled in a descent from 2000 to 4000 m.

The distinctive behaviour of silicate is revealed by diagrams (Fig. 1) relating it to salinity, temperature, density and total phosphorus at station 2659 worked by R.R.S. *Discovery II* on 12 May 1950 (Armstrong, 1951; Cooper 1952, Table IV). The temperature-salinity diagram (Cooper, 1952, fig. 15, to 1500 m. only) suggests that between 1200 and 2000 m. we have to deal with simple mixing of the mean Gulf of Gibraltar and North Atlantic Deep waters. If silicate concentration were subject only to mixing processes the curves in Fig. 1 between these depths would be straight lines. They are not—consequently it would seem that solution of either particulate silica or of aluminosilicates may be occurring. As yet, clear interpretation is not possible. At least five hypotheses may be erected to explain, in whole or in part, the observed distribution: (i) solution of bottom deposits; (ii) solution of 'clay' and of silica in suspension; (iii) concentration by vertical partition; (iv) tundra drainage; (v) sinking of surface water. These are examined in turn.

## SOLUTION OF BOTTOM DEPOSITS

*Discovery* station 2659 was near the continental slope, solution from which could have occurred. The results of Wattenberg (1937) and Koczy (1950), however, suggest that the converse process occurs, adsorption or chemical combination of silicate from the water into the material of the bottom or into hexactinellid sponges.

## SOLUTION OF 'CLAY' AND OF SILICA IN SUSPENSION

The distribution may have come about by solution of minerals of terrigeneous origin. If this were so the content of aluminium should increase with depth in much the same way as does silicate, and a diagram relating silica in solution to aluminium in solution should approach a straight line.

The distribution may also have come about by re-solution of the skeletons of diatoms and radiolarians and the faeces of herbivores feeding on these.

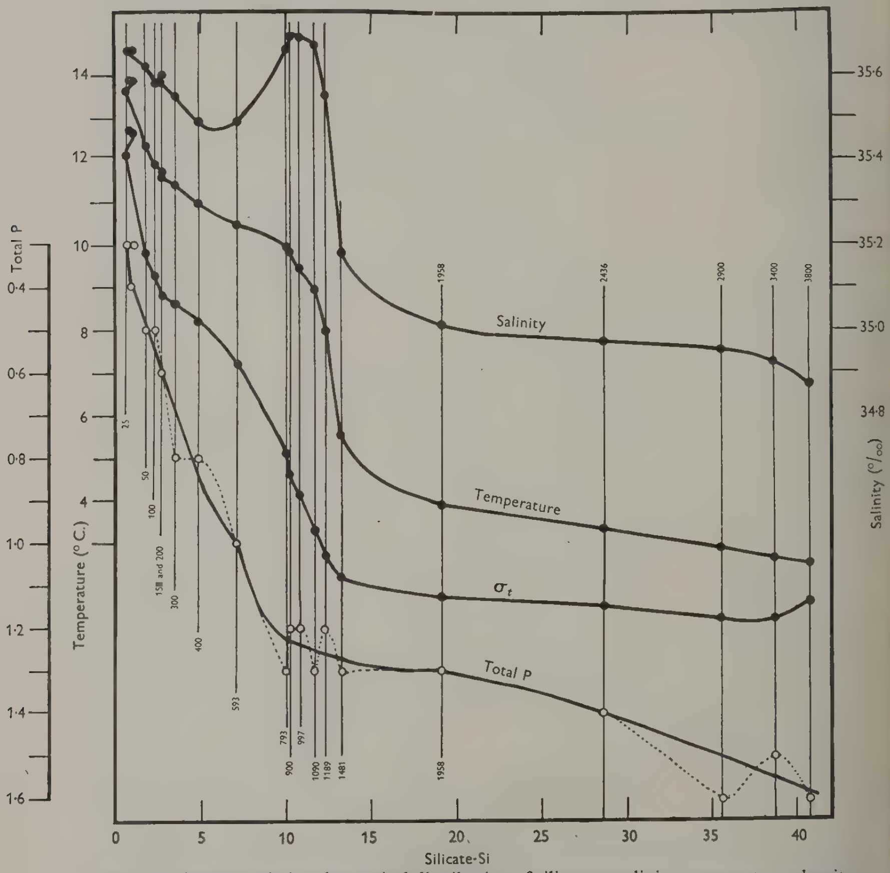


Fig. 1. Diagrams relating the vertical distribution of silicate to salinity, temperature, density, and total phosphorus at *Discovery II* station 2659 on 12 May 1950. Since the results for total phosphorus are less accurate than the rest, its curve has been smoothed. Silicate-silicon (Si) and total phosphorus (P) in $\mu$g.-atom/l. The figures against the thin vertical lines represent depths (in metres).

As the particles dissolve, whether they be of mineral or biological origin, they become smaller, sink more slowly, and expose to the action of the water a greater surface area relative to volume, which favours solution. Wattenberg (1937), who found a similar distribution of silicate in the neighbourhood of the Cape Verde Islands, explained it in this way, whilst Clowes (1938) has produced cogent evidence for the process in the Antarctic. King (1938) stated that most of the reported figures for the solubility of silica in water vary between 700 and 2300 $\mu$g.-atom/l. Correns (1940) measured the variation with pH of the solubility of silica in terms of the fraction able to pass a membrane filter (Fig. 2). By interpolation at pH 8·15, the content of silica in solution was about 5 mg.-atom/l. Si. Natural sea water should never be saturated with silica.

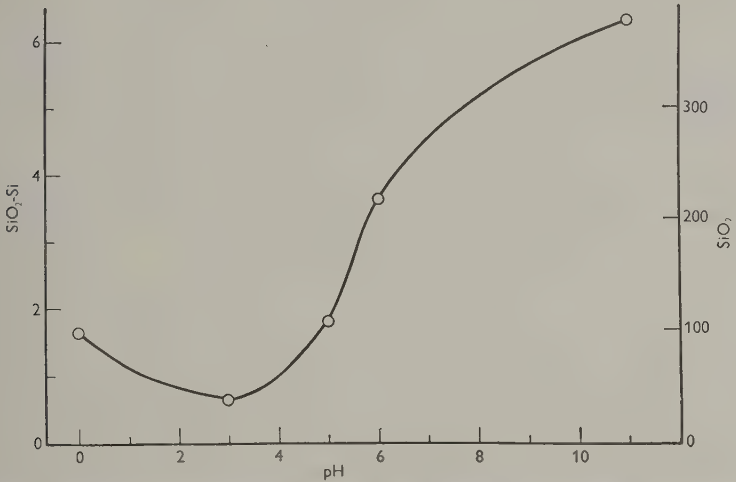


Fig. 2. Dependence of the solubility of silica ($SiO_2$) in water on pH (after Correns, 1940). Silica expressed as mg.-atom/l. silicon (left) and as mg./l. silica (right).

Hart (1934, pp. 11 and 185–6; 1942, pp. 322–39) has marshalled much evidence, circumstantial but strongly supporting the view that re-solution of diatomaceous silica is a speedy process in the sea. He examined (1942, p. 327 and private communication) the stomach contents of *Euphausia superba* and other planktonic animals, and found that the diatom species identifiable were those most strongly silicified, the same that remain recognizable in bottom deposits and in bird guano, such as *Fragilariopsis*, Discoidea (including *Thalassiosira* and also *Coscinodiscus* and *Actinocyclus* spp.), spines of the most robust of all chaetocerids, *Chaetoceros criophilum*, terminal spines of *Rhizosolenia* spp., etc. The more typically oceanic, exceedingly numerous but less strongly silicified forms, including most *Chaetoceros* species, are probably quite as important as food for the planktonic herbivores but are digested too thoroughly to be identified in the stomach contents. These less strongly silicified forms (p. 338) are also very rarely recognizable in the bottom deposits. It is therefore of interest that Wailes (1929) found that the silica content of a collection consisting mostly of small species of *Chaetoceros* was only 40 %, whereas a collection mostly composed of large *Coscinodiscus* contained 75 % on the dry weight.

Again Hart (1942, p. 334) has discussed the removal of phosphate and silicate from Antarctic water by phytoplankton, largely diatoms. He considers that the same process of rapid re-solution of silica is going on there as was proposed for the English Channel (Cooper, 1933, p. 744). There the much lower production of phytoplankton computed from fall in silicate was attributed by the writer to the rapid return and immediate re-use of silica from the previous crop. It is suggestive that the shorter the time interval between sampling and re-sampling at the Antarctic stations the more nearly the crop of phytoplankton calculated from decrease in silicate approached that calculated from decrease in phosphate. Hart also pointed out (pp. 324–6) that in the northern zone of the Antarctic (i.e. immediately south of the Antarctic Convergence) as the silicate content of the upper waters decreases with the advance of spring so does the solenoid diatom *Corethron criophilum* change from a large strongly silicified spinose phase to a less strongly silicified, usually spineless, *inerme* phase.

There is evidence for the insolubility of the silica in diatoms, the result of direct experiment. Diatomaceous ooze is found on the floor of the oceans where the skeletons of strongly silicified species retain through geological ages the delicate markings of the living cell. According to Rogall (1939), the skeletons of marine and fresh-water diatoms consist of pure silicic acid (Kieselsaüre) shown by chemical analysis and X-ray crystallography. The preparation of most of the samples would have removed any organic material which would protect silica against solution. None the less, the recent, chemically untreated sample of the marine diatom *Coscinodiscus concinnus* gave X-ray photographs by the technique of Debye and Scherrer which showed no diffraction rings but only some scattering of X-radiation around the point of penetration of the main beam. This suggests that in geologically recent diatoms no 'crystallites' of significant size are present. In geologically older material annular scattering is to be seen, becoming fairly strong in Miocene diatomaceous earth. As diatomaceous earths age part of the 'sub-colloidal' silica becomes transformed by inner metamorphosis to a micro-crystalline crystal lattice which indicates progressive formation of an opal structure. Such a change would affect solubility.

Atkins and Miss F. A. Stanbury (Atkins, 1945) found evidence for the insolubility of diatom skeletons in sea water even at pH 8 and up to 10·6. Miss Stanbury's earlier observations to the contrary (1931) were based on an error of observation due to the difficulty of seeing nearly transparent diatom skeletons in sea water. Addition of safranin to the water allowed the uncoloured skeletons to be seen. Conger (1941) stated that although diatom shells present a great amount of thin surface to possible solution, the purity of the hydrated silica (also Rogall, 1939) appears to render them resistant to such solution. Diatom shells, once formed, are said to be practically a permanent deposition or fixation of silica. Coupin (1922) studied the freshwater diatom, *Nitzschia linearis*, cultured in Knop agar medium with various sources of silica. Washed sand, gelatinous silica, and alkaline silicates led to no increased growth, whereas in presence of kaolin, felspar and pure clay the cultures flourished. Atkins (1927) has shown the readiness with which soils and disintegrating rocks part with silicate to water; he concludes that solution of silicate most likely takes place from dispersed clay and that the rate of solution of diatom skeletons is too slow to matter. Consequently, he (1945) interprets Cooper's calculation of an apparently low phytoplankton crop from silicate consumption as due not to re-use of silica but to the production of autotrophic flagellates which require no silica and are more abundant than had been previously realized.

There is thus a direct conflict of much well-attested evidence. Is there an unrecognized factor which would allow this apparent conflict to be resolved? In this paper by 'dissolved silicate' we have meant no more than that form of dissolved hydrated silica sufficiently dispersed in sea water to react quantitatively with the standard reagents to form molybdosilicate. This presumably—but only presumably—is identical with the material which diatoms are able to withdraw from the sea to build their skeletons. Much has been written on the nature of 'dissolved silicate', but few clear unassailable conclusions have been drawn. One of the clearest expositions is that of Carman (1940). The metasilicate ion, $SiO_3^{2-}$, almost certainly does not exist. The simplest silicate ion is probably orthosilicate, $SiO_4^{4-}$, or more often $H_nSiO_4^{(4-n)-}$. In all silica compounds the central building bricks are $SiO_4$ tetrahedra linked through oxygen bonds. In vitreous silica, such as exists in colloidal silicates and in diatom skeletons, the tetrahedra are linked to produce a random three-dimensional network.

When sodium silicate is acidified, monosilicic acid is first formed. Molecular weight determinations by several workers have given values between 60 and 150. The lower figure would require that (mono)orthosilicic acid should be 60 % dissociated. The low-molecular silicic acid is believed to condense to long chains of polysilicic acid. The structure which results is heavily hydrated and holds fluid by capillarity and, no doubt, foreign ions also. Treadwell (1935) found that the molecular weight between 149 and 1015 increased at the rate of 22·2 per hour. Tourky (1939, 1942) found that the rate of increase depended upon pH; at pH 11·7 there is no polymerization, but this occurs at pH 10·85 and the rate of polymerization reaches a maximum between pH 6 and 7. The rate and extent fall to a minimum at pH 2·3 in a region much used for the development of yellow molybdosilicate for analytical purposes. In more strongly acid solutions polymerization again becomes more rapid and extensive. At pH 8·32, near that of sea water, 28 % of newly formed silicic acid becomes in 1 hr. unable to pass an ultrafine membrane filter having a time constant of 200–300 min. Hurd & Merz (1946) found that the amount of silica capable of diffusing from a hydrosol through a membrane appears to approach a constant value. They explain this unexpected result as follows. The process of setting a silicic acid gel, whatever it may be, does not run entirely to completion but comprises a series of equilibria very much displaced towards the more complex side. Dialysis removes the simpler particles with a shift in the equilibrium towards the simpler materials. If correct this conclusion has great significance in oceanography if, instead of 'dialysis', we read 'removal of silica by diatoms'. A similar displacement of equilibrium would be achieved under the analytical conditions of determination of silicate in sea water (Hurd, 1938; Correns, 1940).

Tourky & Bangham (1936) recorded that nearly all the silica in Nile and Egyptian well waters and in dilute (20 $\mu$g.-atom/l. silicate-Si) Graham sols was held back by ultra-filters, but that sea water appears to exert a 'peptizing' action akin to that of alkali. Thus, known volumes of a dilute Graham sol of known silica content were added to silica-poor sea water, the quantities being such as to correspond to a silica-rich sea water. After addition of alkali, colorimetric determination returned the correct silicate content. Without addition of alkali 25–100 % of this was found, depending on the age of the solution when the molybdate reagent was added.

Kargin & Rabinovitch (1935) prepared a very pure $SiO_2$ sol by oxidizing silane, $SiH_4$, by ozone in water. This sol was electrochemically neutral, had a pH near to 7, no acidic properties and only a small quantity of compensating ions (*Gegenionen*) in the outer component of the double layer. Thus very pure hydrated silica dispersed in water is not an acid in the sense that hydrochloric acid, boric acid, or even phenol are acids.

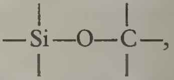
Sols prepared by methods employing electrolytes—and these have been the subject of most investigations and correspond better to the process of solution of silica in sea water—seem always to retain ions of strong electrolytes either tightly bound as part of an electrical double layer or as components of interstitial fluids. The dissociation constants of so-called silicic acid derived from such systems are functions rather of these associated ions of strong electrolytes and vary much from experiment to experiment. Indeed it needs to be proved that orthosilicate ions can persist at the pH of natural sea water.

Carman (1940) described a method of hydration of colloidal silica which would set free hydrogen ions giving the surface of the colloid a negative charge, i.e. converting it into a large anion. The anionic character of such a colloid will depend on size, i.e. on the ratio of surface to volume. A solution of hydrated silica may contain aggregates or particles of every size ranging from an odd orthosilicate ion through $Si_3O_8^{4-}$ to a large diatom skeleton. Viewed in this way attempts to classify silicate in sea water, either in terms of ions all alike, or as all crystalloidal or all colloidal, become meaningless.

The practical problems are: (1) to establish what ranges of colloid particle size down to orthosilicate ion allow 'dissolved silicate' to react quickly to form molybdosilicate under analytical conditions; (2) what ranges are suitable for use by diatoms, radiolarians and sponges; and (3) how the solution or dispersion of large particles to smaller takes place.

Observations by Briscoe, Holt, Matthews & Sanderson (1937) and Kitto & Patterson (1942) are relevant. They established that freshly fractured surfaces of quartz and some mineral silicates are in a highly reactive state and readily yield 'soluble silica' on contact with water. In the sea much the commonest way of exposing fresh silica surfaces by fracturing will occur in the guts of herbivores which grind or triturate their food. During grinding the structure of the surface is disturbed and a layer of more irregular structure, possibly a Beilby layer, is formed. Such a Beilby layer, if formed, would increase with the amount of grinding to become many ångströms thick and would be likely to have a higher solubility than the underlying material. One may visualize the process of solution in the herbivore gut not as like the solution of sugar or common salt, but as one of mechanical attrition by which ever more reactive surfaces may become exposed and by which smaller pieces of colloidal silica, necessarily further hydrated by the process, may be torn from larger ones.

Dr T. J. Hart has made the following comment: 'At depths more than a few hundred metres below the photic zone herbivores cannot be feeding as such. Yet the bathypelagic fauna is very considerable. Obviously it cannot consist entirely of carnivores and their parasites. Detritus feeders ultimately dependent on the rain from above must here be the "key industry" forms. Hence my emphasis on the probability that most diatom skeletons pass through several stomachs on their way down.'

To sum up, the following assertions seem valid. (i) The phrase 'sea water saturated with silica or silicate' has little meaning. (ii) More silica or silicate could be 'dissolved' or held in sea water than is ever present in nature. (iii) Aluminium silicates or 'clay' are concerned in the silica system in sea water. (iv) Hydrated silica in equilibrium in sea water consists of particles of very varying size some of which can penetrate membrane filters and some of which cannot. (v) Aggregated hydrated silica is in the main electrochemically neutral and the acidic properties attributed to it are due to anions held in interstitial fluid, or to electrochemical charges on the surface, or to an electrical double layer arising from the distribution in space of $SiO_4$ tetrahedra and of unsatisfied valencies produced as the result of the process of hydration. Thus the term 'silicate' which suggests the anion of an acid or salt, whilst appropriate at $pH > 12$, is of doubtful validity at the pH of natural sea water: 'dispersed hydrated silica' or 'dispersed silica' may be more fitting terms than 'dissolved silicate'. (vi) If the equilibrium system is disturbed by removal of the simpler particles by dialysis in the laboratory or by diatoms in the sea, more complex particles will slowly yield simpler ones in order to restore the equilibrium. (vii) Polymerization is least in the range of pH commonly used for the development of the yellow molybdosilicate complex in analytical practice. (viii) The chemical constitution of the silica in diatom skeletons is similar to that of hydrated silica dispersed in water. (ix) In spite of this, the skeletons of many but not all species of diatoms are resistant to solution and for all practical purposes are insoluble whilst intact. (x) This insolubility is difficult to understand unless the surfaces of the skeletons are in some way protected against solution by an organic skin. Such a skin has never been demonstrated by chemical or X-ray analysis. Since it would be sufficient to satisfy the residual valencies of the $SiO_4$ tetrahedra in the boundary surface more strongly than does water, a protective layer only a few molecules thick and undetectable chemically would suffice. Postulation of a siloxane bond  $-\overset{|}{\underset{|}{\mathrm{Si}}}-\mathrm{O}-\overset{|}{\underset{|}{\mathrm{C}}}-$, never yet found in nature,[1] would assist the formulation of such a protective coating. (xi) Freshly fractured surfaces of silica are highly reactive and soluble. (xii) The skeletons of diatoms, particularly thin fragile ones, are likely to be so fractured in the guts of herbivores browsing on them. Herbivores and detritus feeders are likely to be responsible for the greater part of the redispersion of hydrated silica frequently reported in the upper layers of sea. (xiii) In surface waters in which diatoms and radiolarians grow and are eaten a true equilibrium involving dissolved or dispersed hydrated silica may never be reached. (xiv) Sea water containing dispersed silica completely in equilibrium is likely to be found only in the ocean abyss. Only abyssal water may be suitable for a study of silica equilibria.

Confronted with the same body of evidence Atkins and the author have on some issues drawn opposed conclusions. The author's opinion is that the conflict is apparent and not real and arises from some condition of the intact diatom skeleton which is not understood. The conflicting lines of argument are presented to stimulate further study of the process of solution of siliceous matter in deep waters, especially in North Polar waters, the Norwegian Sea and the north-western North Atlantic.

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[1] The following information has since been received by the Department of Scientific and Industrial Research in answer to their *Unanswered Question* 67: 'Is there any authentic case of organic silicon compounds having been isolated or detected in living organisms?' (1) T. Takeuchi (*Bull. Coll. Agric., Tokyo*, Vol. 7, pp. 929–31; *Chem. Abs.*, 1907, Vol. 1, p. 2620) reported detecting an organic silicon compound in hay. (2) E. Drechsel (*Chem. Zentrallblatt*, 1897, Vol. 2, p. 666) reported a substance $Si(OC_{34}H_{59}O)_4$ which appears to have been an ester of silicic acid. This compound was, it is understood, isolated from duck feathers and may originate in the oily gland at the base of the tail and be transferred to the feathers during preening. Thus the possible presence of Si—O—C linkages in diatoms may not be without precedent in other living organisms.

It remains for the future to show how great is the effect of solution of silica from siliceous matter compared with the processes to be described.

### Concentration by Vertical Partition

The enormous concentration of silicate in Antarctic waters is much assisted by the vertical circulation (Clowes, 1938). The Antarctic surface water flows towards the north. The water goes on to sink at the Antarctic Convergence but much of the silicate remains behind. It has been removed by diatoms which get eaten by herbivores who need no silica. Siliceous faeces and dead broken frustules sink into the Intermediate Water beneath which, enriched in the writer's view by re-solution, returns to the Antarctic. In the North Atlantic there is a similar Intermediate Water (Wüst, 1936, p. 176). Comparatively it is rudimentary and its progress difficult to follow. The Polar front associated with it makes a seasonal migration of 500–1000 km. None the less, this Intermediate Water working against the Irminger Current above would seem capable of some degree of concentration of silicate. It needs to be shown whether this happens on a scale that matters, and whether the enriched water moves into the region where Nansen (1912) believed the North Atlantic bottom water may be formed in winter.

### Tundra Drainage

The North Polar Sea receives much drainage from the tundra areas of Siberia, northern Canada and Alaska. Under a tundra climate the subsoil is permanently frozen. In summer this stops the normal downward percolation of subsurface water derived from thawing of the soil above and from precipitation (Flint, 1947, p. 459). As a result the thawed mantle becomes saturated with water and flows bodily downhill, a process known as 'solifluction'. Such a climate with hard freezing, shallow thawing, bad drainage, and much solifluction is likely to lead to rapid weathering and comminution of rock particles. Moreover, poor development of humus will hinder the development of a stable soil. Conditions should be very favourable for solution of silica and its transport by summer drainage into the surface waters of the North Polar Sea from which it may escape in the East Greenland Current. This in turn contributes to the mixing areas south-east and south-west of Greenland in which the North Atlantic deep water may be formed. Although the pure Polar water which escapes as the East Greenland Current is, according to Kiilerich (1945, p. 56), poor in nutrients, no silicate analyses have to the writer's knowledge ever been made on it. There is a strong probability that the silicate content will prove to be very high (at least 50 $\mu$g.-atom/l. $SiO_2$-Si). Thus it would seem that a full knowledge of the distribution of silicate in the North Polar Sea, in the East Greenland Current, the north-western Atlantic generally, and in the deeper water of the Norwegian Sea, will be needed for interpretation of deep-water results elsewhere.

Dr H. U. Sverdrup (private communication) has suggested that Antarctic waters should also receive much dispersed silica formed by comminution of rock beneath the very large glaciers of the Antarctic continent.

### SINKING OF SURFACE WATER

Though Nansen's view (1912) that much of the bottom water of the North Atlantic is formed in an area south-east of Greenland around 59–62° N., 38–48° W., has gained wide currency, it has never been finally proved. The observations which he used were not his own and some of them may be suspect. In March 1933 and March 1935, the German research ship *Meteor* ran sections across the area (Defant, Böhnecke & Wattenberg, 1936). The densest surface water (temp. 4·07° C.; sal. 34·96‰; $\sigma_t$, 27·76) was found at station 79 (59° 38′ N., 4° 42·5′ W.), but water at least 1° colder and 0·10 $\sigma_t$-unit heavier was needed to provide satisfactory proof of Nansen's hypothesis. Defant (1936) had stated that a main objective of the *Meteor* cruises was to test Nansen's hypothesis but in the end he has nothing to say on the matter. He would seem to feel that the hypothesis remains unproven. Von Schubert (1935, pp. 35–7) examined the stability at *Meteor* station 76 (29 March 1933; 60° 56′ N., 41° 28′ W.). Down to 800 m. there was no obstacle to vertical mixing, but he also considers that the formation of bottom water there remains an open question.

The extent of formation of bottom water will depend upon the coldness of the winter. Smed (1947, 1948) has recently published monthly anomalies of the surface temperatures in areas of the North Atlantic from 1876 to 1939 (i.e. departures from Ryder's area monthly means for the years 1876–1915). Nansen's postulated region of formation of bottom water lies close to the point of union of Smed's areas B, C and D and mostly within areas B and D. The observations used by Nansen (1912, p. 25) were mostly collected in April 1906, which Smed's tables show to have been very cold (Table I), whereas the *Meteor* worked in years (March 1933 and March 1935) when the water temperatures were 0·5° above the long-term mean. It is therefore probable that temperatures in the late winter and early spring of 1906 were between 1 and 2° lower than in 1933 and 1935. In Table II the densities found by the *Meteor* have been adjusted for conditions 1 and 2° colder than in 1933. Thus, in 1906, the surface water may well have been heavy enough to sink right to the bottom of the Atlantic, and Nansen's conclusion for that year was correct, whereas in 1933 and also 1935 it could not have sunk much below 800 m. Only in 1907, 1918 and 1921 have comparable cold conditions recurred so that formation of North Atlantic bottom water south-east of Greenland may now have become a rare event.

Nansen (1912) showed quite clearly that in the years 1903 and 1910 cold heavy water from the Norwegian Sea flowed into the Eastern Basin of the North Atlantic over the sill of the Faeroe-Iceland ridge at about 64° N., 13° W., a result substantiated in 1938 by the *Dana* (Cons. Perm. Int. Explor. Mer, 1944, p. 119, stations 5954–5957). He also definitely established a similar outflow over the Iceland-Greenland ridge into the Western Basin. Although he considered neither of these outflows adequate to account for the great volume of the cold bottom water of the Atlantic, that over the Faeroe-Iceland Ridge may be locally important for the hydrography of the waters bathing western Europe. The *Meteor*, on 21 March 1933, also found a small area of heavy water (temp. 3·66° C.; sal. 34·99‰; $\sigma_t$, 27·82) on the

TABLE I. MONTHLY ANOMALIES OF TEMPERATURE OF PART OF NORTH ATLANTIC

Departures from Ryder's 'area monthly means' for the years 1876–1915 of the sea surface temperature ° C.) in three areas south-east of Greenland in March and April in years studied by Nansen and by the *Meteor* expeditions; *n* is the number of observations averaged; from Smed (1947, 1948).

| | Area B | | Area C | | Area D | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Latitude range... | 55° N. to coast of Greenland | | 60–66° N. | | 55–60° N. | | Mean of area means | Arithmetic mean of all observations | |
| Longitude range... | 40–50° W. | | 30–40° W. | | 30–40° W. | | | | |
| Mean anomalies | *n* | ° C. | *n* | ° C. | *n* | ° C. | ° C. | Σ*n* | ° C. |
| March 1906 | 4 | −0·7 | 6 | +0·5 | 13 | 0·0 | −0·1 | 23 | 0·0 |
| April 1906 | 64 | −1·1 | 2 | −2·2 | 34 | −1·3 | −1·5 | 100 | −1·2 |
| March 1933 | 13 | −0·1 | 5 | +1·4 | 25 | +0·7 | +0·7 | 43 | +0·5 |
| April 1933 | 82 | 0·0 | 22 | +1·0 | 53 | +0·7 | +0·6 | 157 | +0·4 |
| March 1935 | 19 | +0·3 | 3 | +0·9 | 15 | +0·2 | +0·5 | 37 | +0·3 |
| April 1935 | 76 | +1·0 | 21 | +0·1 | 29 | +0·5 | +0·5 | 126 | +0·5 |

TABLE II. COMPUTED DENSITIES FOR APRIL 1906

Probable densities of the waters south-east of Greenland in April 1906 computed from *Meteor* observations in March 1933 and assuming that surface water temperatures were 1 or 2° C. colder.

| Station no. | Latitude N. | Longitude W. | Observed temperature | Observed salinity | Actual $\sigma_t$ | $\sigma_t$ if temperature lowered by 1° | 2° |
|---|---|---|---|---|---|---|---|
| 76 | 60° 56′ | 41° 28′ | 4·67 | 35·00 | 27·72 | 27·85 | 27·94 |
| 78 | 60° 12·5′ | 41° 52·5′ | 4·21 | 34·91 | 27·69 | 27·82 | 27·91 |
| 79 | 59° 38′ | 40° 42·5′ | 4·07 | 34·96 | 27·77 | 27·86 | 27·95 |

West Icelandic island shelf at 65° 17′ N., 25° 30′ W. heavy enough to cascade to a great depth. Jacobsen (1943), in his account of the water movements through the Faeroe-Shetland Channel, makes no mention of any outflow over that sill into the Atlantic, and no evidence for it was found by the *Explorer* in 1933 and 1935 (Cons. Perm. Int. Explor. Mer, 1934, p. 67; 1935, p. 69).

Smith, Soule & Olav Mosby (1937; see also Dunbar, 1951) suspect that the bottom water of the Labrador Sea is formed in winter in a restricted area of that sea centred on 60° N., 55° W., and discuss its rather complex origin in so far as this can be surmised from summer observations. They point out that 'our deep water which evidently drains out of the Labrador Basin into the North Atlantic embraces what Wüst (1936) has designated as North Atlantic deep water'. Wüst himself (1936) also leaves the origin of the North Atlantic bottom water as unsolved. It would seem that only in one year in ten are temperatures low enough to produce water heavy enough to sink to the bottom of the Atlantic, and that attention would be better focused on the Labrador Sea rather than on the waters south-east of Greenland.

Since direct winter observations in these uncharitable waters are hard to come by, an alternative means of search for the origin of the North Atlantic bottom water should be welcome. This may well be provided by determinations of silicate by the quick and accurate method now available (Armstrong, 1951). For reasons already given, the postulated high silicate content of the fresh waters draining from the tundras should mark in turn the East Greenland Current, the Labrador Current and the waters of the Labrador Sea with distinctive contents of silicate. The deeper water of the Norwegian Sea may also acquire a high and characteristic content of silicate. In all these, except in surface water above the thermocline, content of silicate may be reasonably assessed in summer.

To enter the basin of the Eastern North Atlantic directly, heavy water from either south-east of Greenland or from the Labrador Sea would need to cross the mid-Atlantic Ridge in a region where its depth is about 3000 m. According to Wüst's charts (1936, Beilage LVI, LVII, LXXI and LXXII) the temperature there exceeds 2·9° (potential temperature 2·64°) and the salinity exceeds 34·96‰, whereas the water abreast of the English Channel between 3000 and 4000 m. has a lower temperature, 2·5–2·7° (potential temperature 2·15–2·45°) and a lower salinity of 34·90–34·92‰. There is no obvious passage north of 24° N. for bottom water from the north-western Atlantic to cross the Ridge into the Eastern Basin so that such water must needs approach Europe from the south. The water which the *Dana* observed entering the Atlantic from the Norwegian Sea across the Faeroe-Iceland Ridge in 1938 was cold enough but was 0·08‰ too saline. Consequently, the origin of the bottom water west of Europe is still uncertain.

The Antarctic bottom water extends well north of the Equator. Wüst (1936, Abl. 16) pictures it as extending to 40° N. in the Western Basin and to 25° N. in the Eastern. His conclusion is based largely on an apparent density inversion widely recorded below 4500 m. Since a true inversion is very unlikely, he attributes the phenomenon to a breakdown in Knudsen's equation, $S = 0{\cdot}030 \times 1{\cdot}8050\ Cl$, when applied to the bottom water of the Atlantic.

Sverdrup (1929, p. 129) had shown that the brine which becomes enclosed in sea-ice when it freezes retains relatively more chloride than other salts leaving the unfrozen water relatively deficient by about 0·02‰ Cl. The true density of this water measured directly is about 0·03 $\sigma$-unit heavier than that computed from salinity and temperature by Knudsen's tables. When such water becomes admixed with Atlantic water to form North Atlantic deep water this anomalous property will become incorporated. The Antarctic bottom water arising more directly by a similar freezing-out process in the Weddell Sea (Deacon, 1937) would seem, according to Wüst, to have acquired an even greater chlorinity-density anomaly. The result is that in the deep water of large areas of the Atlantic, water of slightly greater computed density overlies lighter. When this occurs Wüst suggests that North Atlantic deep water overlies Antarctic bottom water.

There is abundant evidence that the Northern Hemisphere is warming up (*inter alia*, Helland-Hansen, 1949; Defant & Helland-Hansen, 1939; Cooper, 1952, p. 501), a state of affairs which in the area south-east and south-west of Greenland in winter should slow down the rate of formation of the North Atlantic deep water. Less should be sinking to the ocean abyss than in years past. Much less is known about any similar warming up in the Antarctic and Southern Oceans, but the huge reserves of ice there should slow down the process. Consequently, in a struggle between North Atlantic and Antarctic bottom waters, victory would be expected to go to the Antarctic water. There should to-day be a marked tendency for Antarctic bottom water to spread northwards in the Atlantic and to fill the Eastern basin to a greater depth. At *Discovery II* station 2659 the water at 3800 m. (salinity 35·87‰, computed density $\sigma_t$ 27·84, computed potential density $\sigma$ 27·87) is apparently lighter than the water at 3400 m. by 0·03 $\sigma_t$ -unit. Error in any single result is always likely but, at least, the need is indicated for fresh deep observations in the Eastern North Atlantic. Since the presence of Antarctic water is in question, determinations of silicate may be of much value.

Locally down to 1200 m. near the continental slope of the eastern North Atlantic the distribution of silicate will be affected by cascading in winter and by capsizing of water masses, processes which are under investigation.

Thanks are due to the National Institute of Oceanography and to Dr H. P. F. Herdman and his colleagues of R.R.S. *Discovery II*, who obtained the water samples and to Mr F. A. J. Armstrong, who made the analyses.

## Summary

The distribution of silicate at the deep *Discovery II* station No. 2659 west of Ushant between 1200 and 2000 m. cannot be attributed to simple mixing of 'Gulf of Gibraltar' water and North Atlantic Deep water as can the distribution of some other constituents. Moreover, between 2000 and 4000 m. the concentration of silicate is doubled. Five hypotheses have been examined which may bear on the distribution of silicate.

The chemistry of silicate dispersed in water has been examined with respect to the possible solution of aluminosilicates and of intact and fractured diatom skeletons in sea water. Conclusions have been summarized.

Solution of silicate from, and removal by, the sea bottom and concentration within the sea by vertical partition are severally discussed.

Reasons are presented for believing that drainage from the tundras of the Northern Hemisphere should yield very large amounts of silicate to the North Polar Sea. From this initial hypothesis further oceanographical deductions have been drawn.

The evidence for the formation of North Atlantic Bottom Water at the sea surface south-east of Greenland, first proposed by Nansen, has been re-examined in relation to the movement of dissolved silicate. It is suggested that in the cold spring of 1906, from which year Nansen drew most of his data, his conclusion was probably sound, but that in most years sufficiently cold surface conditions are not attained.

The probable effect of the warming up of the Northern Hemisphere in recent years on the deep circulation of the Atlantic is reviewed.

It is suggested that the great variations which occur in the concentration of silicate in the sea should be of use in interpreting the nature and movements of the major ocean water masses.

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# ON THE BIOLOGY OF *CALANUS FINMARCHICUS.* VII. FACTORS AFFECTING EGG PRODUCTION

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(Plate I and Text-figs. 1–5)

Comparatively little is known about the factors affecting egg-laying in *Calanus*. Deductions from work in the field have been made by Nicholls (1933 *a*, *b*) and Marshall, Nicholls & Orr (1934), and experimental work in the laboratory has been done by Raymont & Gross (1942).

## EGG-LAYING IN *CALANUS*

The anatomy of the reproductive system has been described in detail by Lowe (1935). In the female there is a pair of diverticula extending from the proximal end of the oviduct into the head region, and into this the developing eggs pass. Each diverticulum has a dorsal and a ventral channel, and the eggs pass from the dorsal into the ventral channel and then into the oviduct proper. The oviduct rises from the forward end of the ovary and crosses the body laterally and ventrally so that a short part of it can be clearly seen.

The state of development of the eggs can be seen in the living *Calanus*, and four stages have been described by Marshall *et al.* (1934); these are, early, medium (Pl. I A), mature and spent. It has been found convenient to make a further division between the medium and the mature, namely the semi-ripe. In the immature female the ovary is small and in the oviduct there is only one row of small eggs. As the ovary enlarges the two diverticula also enlarge and become filled with eggs. In the medium state the dorsal channels of the diverticula are filled with enlarging eggs, and the eggs in the oviducts also increase in size and number. The diverticula gradually fill up until the whole of the space in the head is full of enlarging eggs; this may be called the semi-ripe stage. In the mature female (Pl. I B) the most ventral rows of eggs are larger than those in the rest of the diverticula, and similar large eggs are also seen in the oviducts which have now developed secondary pockets projecting towards the body wall (Lowe, 1935). Before laying (sometimes as much as 48 hr. before) these large eggs swell still further, become granular in appearance and turn slightly orange-pink in colour. Just before laying the pink colour usually deepens, the nucleus disappears and the eggs are then squeezed out through the genital aperture as a string of roughly pear-shaped masses which separate and round off within a minute or two (Pl. I D–F).

Raymont & Gross (1942) state that 'the ova which were extremely small in the narrow oviduct were seen to swell almost instantaneously after extrusion to form oval or slightly irregular shaped eggs of very much greater volume; in fact each egg attained a volume greater than that of all the 30–40 eggs inside the oviduct, obviously by a rapid imbibition of water'. Lowndes (1943) also states that whereas the diameter of the largest eggs in the oviducts is $61{\cdot}5\,\mu$, the diameter of eggs 18 hr. after extrusion is $171\,\mu$. Pl. I C, however, shows the oviduct in a ripe *Calanus* with large eggs almost ready for spawning, and it will be seen that they are much the same size as those being laid (Pl. I D). Several other stages in egg-laying are also shown. In a ripe female the pressure in the diverticula and oviducts causes the eggs to assume an irregular shape, often almost square in side view, and it is impossible to measure the volume accurately. Approximate measurements made on about a dozen eggs from several ripe females gave a volume very much the same as the shed eggs. Thus 5 eggs from a single ripe female had volumes ranging from $1{\cdot}12 \times 10^6$ to $1{\cdot}45 \times 10^6\,\mu^3$, whereas the same batch of eggs, when measured after they had been laid about half an hour later, had an average volume of $1{\cdot}59 \times 10^6\,\mu^3$ (diameter $145\,\mu$). It is probable that Lowndes was measuring unripe eggs. The size he gives ($171\,\mu$ diameter) is that of *C. helgolandicus*, which is the predominant form at Plymouth (Russell, 1951). The process of laying a batch of eggs which may consist of anything up to 150 (though usually 20–60) occupies quite a short time—usually under a quarter of an hour and sometimes only a few minutes. In the laboratory a batch of eggs was usually found in one clump which indicates that the *Calanus* remains passive during the process. After laying, the appearance of the *Calanus* may go back to the semi-ripe state again if all the large eggs have been extruded.

Occasionally eggs were laid which were abnormal. Sometimes they went opaque at once, sometimes they appeared to have no membrane and at a touch collapsed into a viscous drop of protoplasm; sometimes they extruded part of their substance as a very small droplet. These small spheres were observed by Raymont & Gross (1942), who took them for newly laid eggs. Occasionally, also, in a batch of eggs one will be twice or three times as large as the rest. These large eggs may begin to develop but never hatch. J. P. Harding's observations (personal communication) suggest that they are diploid or polyploid eggs. After *Calanus* has been kept in the laboratory for some time the laying of abnormal eggs becomes more frequent.

A number of females were found in which the reproductive organs were in the same state as in the ordinary Stage V. Occasionally a Stage V is seen with a large ovary and well-developed eggs in the diverticula, but as a rule the gonad is very small, no diverticula are visible and the genital ducts are thin cords with no eggs in them. Some of these very immature females may have been newly moulted, but this category also contains the infertile, the parasitized and the abnormal. They are often characterized by an unusually marked development of red pigment at the posterior end of the cephalothorax. Thirty-eight of them were kept and fed to see if they would eventually produce eggs, but most of them died without doing so. In some the ovaries became obviously abnormal and in several a nematode became visible in the body cavity after a few days. Twelve reached maturity and laid eggs, one in 7 days, two in 9, one each in 15 and 16, two in 17, one each in 18 and 19 and three in 20 days.

In view of Rees's (1949) discovery that two forms of *Calanus* were present in the North Sea, those in our hauls in the Clyde sea area were examined. It was found that there were usually a few *helgolandicus*, but the proportion was never more than 5–10 %. In the course of egg-laying experiments it was observed that some females were laying eggs decidedly larger than the majority, and on examination these females were found to be *helgolandicus*. The difference in size extends also to the nauplius. The result of a measurement of 25 of each type of egg laid on 14 March 1950 is shown in Table I. There is a certain variation in size even in the eggs laid by *finmarchicus*, but there is usually a clear difference between the two types. Occasionally, however, eggs of intermediate size were seen and these were laid by *finmarchicus*. No experiments on interbreeding were made, but Rees has suggested that it may take place and if so an intermediate size of egg might be one result. Of 683 females of the over-wintering stock laying eggs in our experiments 4·1 % were *helgolandicus*. No *helgolandicus* were seen among the first generation females.

TABLE I. SIZE OF EGGS IN *CALANUS FINMARCHICUS* AND *C. HELGOLANDICUS*

| *finmarchicus* | | *helgolandicus* | |
|---|---|---|---|
| Size (μ) | No. of eggs | Size (μ) | No. of eggs |
| 138–142 | 2 | 159–163 | 0 |
| 142–146 | 13 | 163–168 | 1 |
| 146–151 | 8 | 168–172 | 10 |
| 151–155 | 2 | 172–176 | 10 |
| 155–159 | 0 | 176–181 | 3 |
| | | 181–185 | 1 |

The *Calanus* for experiment were usually obtained in the afternoon off Garroch Head at a depth of 50–100 m. in a coarse silk tow-net. They were sorted shortly after capture and the selected females kept singly in small crystallizing dishes of 25 ml. capacity. The volume of water used was about 20 ml. They were usually kept in ultra-filtered water or ultra-filtered water with culture added. The sea water was collected off Keppel Pier and filtered through a 'Gradocol' membrane of average pore diameter 0·9 μ. *Calanus* kept in this without addition were considered to be starved. The medium was changed every second day and in these conditions the *Calanus* lived well and if suitably fed, sometimes for months. After a long time, those kept in culture tended to develop surface growths in the form of a dense mat of minute unidentified organisms, probably largely bacterial. Sometimes the growth would envelop the whole of the cephalothorax and the *Calanus* might live like this for some weeks, although it would become very sluggish. Only healthy specimens were used but, when the required type was rare, rigorous selection was not possible and specimens therefore often lacked caudal furcae, or the tips of their antennae, and sometimes lacked spines or even joints on some of the pleopods. They lived well in spite of these injuries and, indeed, it is surprising how much a *Calanus* will endure.

When set up in small dishes in the evening practically all the 'mature' *Calanus* had laid by the next morning (see p. 536), although Harding (Harding, Marshall & Orr, 1951) observed that few mature females fixed during the day contained completely ripe eggs. His criterion of ripeness was the reaching of the full metaphase of the first reduction division, which is the stage reached when the eggs are laid. It was therefore decided to examine *Calanus* hourly to see if there was a restricted time for egg-laying. One hundred and four ripe female *Calanus* picked out from a tow-netting taken at 4 p.m. off Garroch Head between 50 and 100 m. (with 75 fathoms of warp out) were set up about 6 p.m. each in a separate dish of ultra-filtered sea water. They were kept in a cool aquarium and examined at hourly intervals throughout the night. No attempt was made to keep them entirely in the dark. The production of eggs is shown in Table II. Only three had spawned by midnight, 68% spawned between 12 midnight and 3 a.m. and most of the remainder before 4 o'clock. Of the total only five did not lay. The number of eggs laid per *Calanus* was remarkably constant, the average being about 40.

TABLE II. DIURNAL EGG PRODUCTION 19–20 MARCH 1951.
TOW-NETTING TAKEN 4 P.M., 19 MARCH. 104 *CALANUS*

| Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch | Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch |
|---|---|---|---|---|---|---|---|
| 19 | 0 | 0 | — | 4 | 14 | 583 | 41·6 |
| 20 | 0 | 0 | — | 5 | 4* | 120 | 40·0 |
| 21 | 0 | 0 | — | 6 | 2 | 33 | 16·5 |
| 22 | 0 | 0 | — | 7 | 1 | 28 | 28·0 |
| 23 | 1 | 36 | 36·0 | 9 | 2 | 70 | 35·0 |
| 24 | 2 | 79 | 40·0 | 12 | 0 | 0 | — |
| 1 | 24* | 817 | 37·1 | 15 | 0 | 0 | — |
| 2 | 27* | 1165 | 44·8 | 18 | 0 | 0 | — |
| 3 | 20 | 911 | 43·4 | 21 | 1 | 15 | 15·0 |

* One laid whose eggs were not counted.
Numbers below 5 not included in average.

These rather surprising results might have been caused by the disturbance of capture and examination or else, since they were caught at a considerable depth, by the sudden decrease in pressure. Another tow-netting was therefore taken at the same place but slightly nearer the surface (with only 50 fathoms of warp out) at 4 a.m., fifty ripe females were picked out into separate dishes and these were examined every 3 hr. Although a smaller total number of eggs was laid and the peak of production was not so marked, spawning again took place mainly during the early morning (Table III). Thirteen of the fifty did not lay. The smaller number of eggs laid may be caused by the longer period of starvation in ultra-filtered water. It will be shown later (see Table VI) that starvation may have a marked effect on egg production even as early as the second day.

Each *Calanus* was discarded after it had laid unless the number of eggs was very small. Several laid small numbers in consecutive hours (e.g. 6 + 8 + 10 and 5 + 18), but one laid 28 and 34 with an interval of 18 hr. between. The great majority, however, are unlikely to have laid again before the following night.

TABLE III. DIURNAL EGG PRODUCTION 20–21 MARCH 1951.
TOW-NETTING TAKEN 4 A.M., 20 MARCH. FIFTY *CALANUS*

| Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch | Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch |
|---|---|---|---|---|---|---|---|
| 9 | 2 | 103 | 51·5 | 3 | 9 | 275 | 30·0 |
| 12 | 2 | 49 | 24·5 | 6 | 12 | 304 | 30·7 |
| 15 | 2 | 33 | 16·5 | 9 | 3 | 143 | 35·8 |
| 18 | 0 | 0 | — | 12 | 1 | 58 | 58·0 |
| 21 | 2 | 94 | 47·0 | 15 | 0 | 0 | — |
| 24 | 4 | 137 | 39·3 | | | | |

Numbers below 5 not included in the average.

In an experiment in February 1950 on the feeding of *Calanus* throughout 24 hr., six out of ten unselected females laid as follows: one between midnight and 2 a.m., four between 2 and 4 a.m. and one between 4 and 6 a.m., thus confirming the more detailed experiments of 1951. *Mesopodopsis* and *Squilla* have also been found to lay only during the night (Nair, 1939, 1941).

In the Clyde sea area *Calanus* of the first generation are found close to the surface in May (Marshall *et al.*, 1934), and since this change of habit may make a difference in their egg-laying behaviour a similar experiment was done on 30 April to 1 May 1951 when the first generation had reached maturity. The results are shown in Table IV, and it will be seen that in contrast to the overwintering stock this generation laid throughout the 24 hr. Some *Calanus* are found also in deep water at this time, and the experiment was repeated using fifty ripe females from deep water (below 50 m.) and fifty from the top 2 m. Both lots behaved in the same way, laying throughout the 24 hr.

Another difference between the winter and the first-generation females is that far more (29%) of the May females laid second batches of eggs within 24 hr. and five even laid a third batch. The average number of eggs laid in the first batch was 61·3, in the second 41·7, and in the third 28·0. In the majority the second batch was laid within 10–15 hr. after the first. This difference may have been caused by the fact that during May the sea was very rich in diatoms.

In 1950, to find the total number of eggs which can be produced by a female, those carrying spermatophores (which, since fertilization takes place soon after moulting, may be assumed not to have laid any eggs) were kept in separate dishes in a refrigerator at about 5° C., fed regularly and examined daily. In all of them the spermatophore was lost after the first day or two. One or two laid also within the first day or two, and, since females normally take a week or two to mature the eggs, these must have been fertilized late when the eggs were almost mature. Most remained for 1 or 2 weeks without laying. This in itself was a disadvantage, for conditions in the laboratory were presumably not so healthy as in the sea. From June onwards, therefore, to avoid delay in egg production, they were kept in an aquarium room at a temperature of about 16° C.

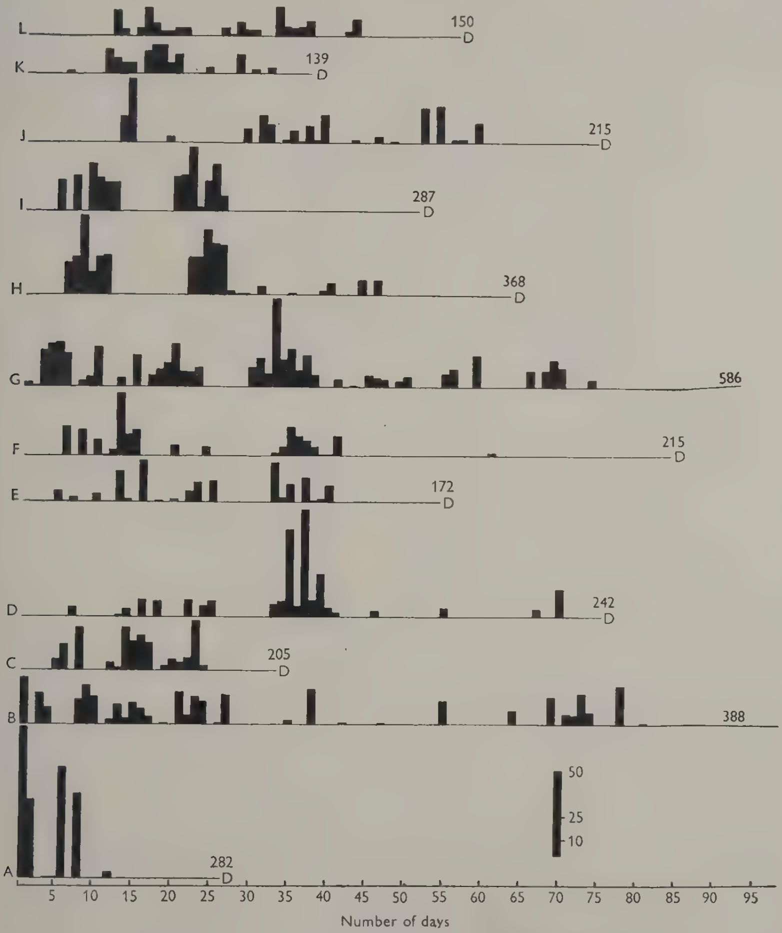
Table IV. Diurnal Egg Production 30 April–1 May 1951. Tow-netting taken 11 a.m. Ninety-nine *Calanus*

| Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch | Time (hr. G.M.T.) | No. of *Calanus* laying | Total egg production | Av. no. eggs/batch |
|---|---|---|---|---|---|---|---|
| 15 | 15 | 916 | 61·1 | 3 | 0 | 0 | — |
| 16 | 6 | 387 | 64·5 | 4 | 0 | 0 | — |
| 17 | 1 | 78 | 78·0 | 5 | 4 | 307 | 76·8 |
| 18 | 14 | 881 | 62·9 | 6 | 2 | 93 | 46·5 |
| 19 | 6 | 373 | 62·2 | 7 | 0 | 0 | — |
| 20 | 6 | 430 | 71·7 | 9 | 4 | 240 | 60·0 |
| 21 | 8 | 512 | 64·0 | 10 | 3 | 144 | 63·0 |
| 22 | 6 | 406 | 67·7 | 11 | 3 | 211 | 70·3 |
| 23 | 5 | 340 | 68·0 | 13 | 2 | 129 | 62·5 |
| 24 | 2 | 69 | 34·5 | 14 | 2 | 118 | 59·0 |
| 1 | 3 | 162 | 54·0 | 15 | 0 | 0 | — |
| 2 | 2 | 109 | 54·5 | 16 | 0 | 0 | — |

Numbers under 5 not included in the average.

The results given by those which laid most are shown in Text-fig. 1. The majority laid several hundred eggs over periods up to 80 days. The most prolific was brought in on 16 June, laid 586 eggs over a period of 74 days and was still alive on the 93rd day. From the diagram it is readily seen that egg production often takes place in a series of bursts lasting about a week. These bursts tend to occur at intervals of about 2 weeks and it seemed possible that they might be related to the phases of the moon. In some of the *Calanus* the egg-laying periods do seem to begin 2 or 3 days after new and full moon, but in others no relation can be made out. The number laid each day varies from 1 up to about 70, but after about the 40th day the numbers both of eggs and of days on which laying occurs decrease. The eggs were usually kept for a day or two and, although at the beginning they were all normal and produced healthy nauplii, as the experiment went on the number of abnormal or unhealthy eggs increased. However, eggs produced after as much as 68 days in the laboratory did hatch, showing that one fertilization is enough for the whole period of egg production by a female.

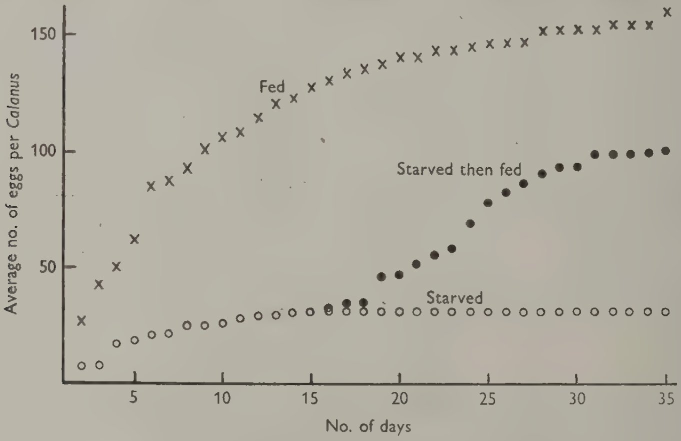
It is of course impossible to say how far this pattern is natural for the sea. In the laboratory they had a continuous ample supply of food, whereas in the sea the amount would be much less and probably sporadic (see, however, p. 543). In the sea, on the other hand, *Calanus* has many enemies at each stage, and few females will survive to lay all their eggs.



Text-fig. 1. Total number of eggs laid by individual *Calanus*. A: 5. v. 50; B: 13. vi. 50; C–F: 15. vi. 50; G: 16. vi. 50; H, I: 27. vi. 50; J: 7. vii. 50; K, L: 26. vii. 50.

## The Effect of Food on Egg-laying

Many workers have discussed the connexion between maxima of phytoplankton and zooplankton. Marshall *et al.* (1934) suggested that broods of *C. finmarchicus* depended for their survival on the presence of diatoms at the time the young brood was growing up. Wimpenny (1937) concluded that phytoplankton-rich water served as a breeding and nursery ground, although adults apparently avoided it. Ussing (1938) showed that in East Greenland, where there is only one diatom increase in the year, copepod reproduction was entirely dependent on it. More recently Wiborg (1940) found a possible connexion between spawning of *Calanus* and an abundant phytoplankton.



Text-fig. 2. Egg-laying in starved and fed *Calanus*.

During 1950 and 1951, when females were laying eggs freely, it was thought of interest to see whether they would lay better when fed than when starved. A number (thirty-two) of female *Calanus* were taken from the sea at the end of April 1950, put singly into the usual small dishes and examined daily for egg production. To avoid the effect of fluctuating temperature they were kept in a refrigerator at about 5° C. Half were starved by keeping them in ultra-filtered sea water and half were kept in ultra-filtered sea water enriched by *Chlamydomonas*. The experiment lasted for 35 days, but after 15 days the starved *Calanus* were divided into two lots; seven of them were now fed and the remaining six continued starved. After the 30th day conditions deteriorated rapidly, and the majority of the *Calanus* died. At the end only four survived in the fed, four in the starved then fed, and two in those starved all the time. The results are given in Text-fig. 2, where the total number of eggs laid per living *Calanus* is shown. There was a large production of eggs on the first and second days, and for reasons stated later (p. 536) these have been ignored in the calculations. Thereafter the production of eggs by the fed was always greater than that by the starved; indeed after a week few of the starved were laying at all. The production of eggs in the fed *Calanus* fell away considerably after 2 weeks, and after the 25th day only two of them were still laying. The average number of eggs produced per fed *Calanus* (ignoring the first 2 days) was 109·8. In the starved *Calanus* it was 23·7, and only one egg was produced after the division into two batches on the 15th day. On the other hand, the starved *Calanus* which were given food produced a total of 92·6 eggs per *Calanus* of which 69·0 were laid after they were fed. Thus, in spite of the deteriorating conditions, feeding the starved *Calanus* resulted in an egg production not much below that of those fed all the time. It looks as if the eggs had been retained until feeding conditions were favourable.

A similar experiment lasting 36 days and giving similar results was done at the same time, keeping however three *Calanus* in each of twenty larger dishes which held about 50 ml. of water. In this the average number of eggs per *Calanus* was: in the fed 106·5; in the starved 20·1 (only three per *Calanus* were laid after the 15th day when the starved were divided into two lots as before); in the starved and then fed, 17·1 before and 40·2 after feeding. The condition of the gonads was examined at the end of this experiment. In the fed the majority still had large eggs in the oviducts, although in one or two the ducts had shrunk. In the starved all had shrunken oviducts, but in those starved then fed all except one had large eggs.

These two experiments were made with females which may or may not have laid before they were caught. One or two indeed, which did not lay during the experiment, may already have completed their egg-laying, and this may account for the smaller total numbers laid when compared with the females of Text-fig. 1.

One interesting fact is that even the starved *Calanus* retained fat up to the end of the experiment. Most *Calanus* have a store of fat (Lowe, 1935) in a sac which lies along the gut. Sometimes, especially in Stage V, this is a large bolster-like mass, sometimes only a small globule restricted to the hind end of the gut. Female *Calanus* on the whole carry less fat than Stage V, that in the anterior part of the sac usually disappearing gradually as the eggs develop. When mature, however, and under starvation conditions, the fat evidently does not go towards making more eggs but is retained by the animal.

The effect on egg-laying of food in general and of different kinds of food was investigated. The following organisms were used: *Coscinodiscus centralis* Ehrenberg, *Lauderia borealis* Gran, *Skeletonema costatum* (Greville), *Rhizosolenia delicatula* Cleve, *Ditylum brightwelli* (West.), *Chlamydomonas* sp. (Dr Parke's *Chlamydomonas* I), *Hemiselmis rufescens* Parke, *Dicrateria inornata* Parke, *Syracosphaera carterae* Braarud, *Gymnodinium* sp., *Peridinium trochoideum* (Stein) Lemm., and *Chlorella stigmatophora* Butcher.

As a standard food a culture of *Chlamydomonas* was used; some animals were also starved in ultra-filtered sea water.

In January and part of February 1951 the females obtained were almost all immature or medium stage and these were used for feeding experiments. Apart from a few specimens (which were probably wrongly diagnosed as immature) most of the immature when fed did not lay until about the 4th day, after which egg production gradually increased. The starved laid no eggs at all.

In a typical experiment lasting from 9 to 16 February the egg production of twenty immature *Calanus* was 17, 0, 0, 69, 144, 141, 179 on successive days, whereas twenty starved produced no eggs over the same period.

A number of experiments were also done about the same time on medium-stage and semi-ripe *Calanus*. These probably included quite a range of degrees of ripeness. Usually one or two laid eggs on the first day, and the number of eggs and of laying females increased from then on. In a typical experiment lasting for 7 days the egg production by twenty fed *Calanus* on successive days was 26, 72, 149, 193, 178, 155 and 66, a total of 839. In twenty starved it was 26, 17, 2, 19, 13, 1, 14, a total of 92.

From the middle of February onwards, ripe females became more abundant and were used for a long series of experiments using different kinds of food.

On the morning after an experiment had been set up there was always a large number of eggs in nearly all the dishes whether the *Calanus* had been fed or not. Apparently the shock of capture and examination stimulates a ripe female to lay. The first day's results are therefore not taken into account in the calculations of the average numbers produced with different foods. The great majority of the *Calanus* in the experiments did lay some eggs, and those which were given suitable food both laid more often and produced more eggs than the starved. Some of the cultures used as food were as good as *Chlamydomonas*, and in others the *Calanus* produced no more eggs than when starved. The organisms are of different size and no attempt was made to equate the volume of food given, but the concentration was always very much richer than anything the *Calanus* would find under natural conditions.

Table V shows a typical experiment comparing the eggs produced by *Calanus* fed on *Chlamydomonas*, *Hemiselmis*, *Syracosphaera* and *Ditylum* with starved *Calanus*. It is apparent that (omitting egg production on the first day) *Ditylum*, *Chlamydomonas* and *Syracosphaera* are all effective foods, whereas giving *Hemiselmis* is little better than starvation. In it they produced fewer faecal pellets than with *Chlamydomonas*. With the starved *Calanus* only one or two faecal pellets were produced and these were very small and almost transparent. With *Chlamydomonas* they were well compacted and dark, with *Ditylum* (as with all diatoms tested) and with *Syracosphaera* they were larger and paler.

It will be seen that there are individual variations in the *Calanus* and that with suitable food some lay every day and some most days. Raymont & Gross (1942) assumed that when a *Calanus* laid on two successive days, one period of egg-laying had been interrupted. Table V and Text-fig. 1 show, however, that with suitable food laying on several days running is quite normal (see also p. 532). The batches laid on succeeding days are often quite large but occasionally a small number appears, often only one or two. A number of eggs ripen together in the oviduct, but possibly for some reason they are not all laid at once and the few remaining are extruded later. For this reason numbers under five are omitted in calculating the number per batch.

TABLE V. EGG PRODUCTION IN INDIVIDUAL *CALANUS* USING DIFFERENT FOODS. 22–29 MARCH 1951

(Experiments run simultaneously with fifteen animals in most.)

| | | *Calanus* | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Day | Food | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | XIII | XIV | XV | Total |
| 1 | *Chlamydomonas* | 25 | 72 | 17 | 16 | 26 | 3 | 22 | 14 | 17 | 10* | 0 | 30 | 63 | 0 | 41 | 356 |
| 2 | | 36 | 0 | 0 | 0 | 1 | 31 | 0 | 28 | 2 | 17* | 0 | 0 | 1 | 0 | 24 | 140 |
| 3 | | 40 | 0 | 31 | 29 | 0 | 35 | 19 | 30 | 0 | 4* | 88 | 6 | 44 | 27 | 26 | 379 |
| 4 | | 56 | 51 | 0 | 0 | 36 | 1 | 0 | 16 | 0 | 13* | 0 | 7 | 0 | 19 | 0 | 199 |
| 5 | | 19 | 44 | 24 | 0 | 1 | 0 | 23 | 8 | 0 | 0* | 32 | 1 | 0 | 0 | 20 | 172 |
| 6 | | 10 | 0 | 8 | 30 | 4 | 1 | 25 | 18 | 0 | 3* | 0 | 50 | 0 | 18 | 17 | 184 |
| 7 | | 9 | 0 | 18 | 0 | M. | 0 | 1 | 0 | 0 | 0* | 0 | 0 | 20 | 0 | 17 | 65 |
| | Total | 195 | 167 | 98 | 75 | 68 | 71 | 90 | 114 | 19 | 47 | 120 | 94 | 128 | 64 | 145 | 1495 |
| 1 | *Hemiselmis* | 32 | 25 | 32 | 80 | 51 | 10 | 12 | 27 | 30 | 74 | 0 | 2 | 41 | 39 | — | 455 |
| 2 | | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | — | 6 |
| 3 | | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | 15 |
| 4 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 11 | 0 | 0 | 0 | 0 | 5 | — | 20 |
| 5 | | 30 | 1 | 0 | 15 | 24 | 4 | 0 | 0 | 0 | 0 | D. | 0 | 0 | 0 | — | 74 |
| 6 | | 0 | D. | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | — | D. | 0 | 9 | — | 16 |
| 7 | | 0 | — | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | 0 | 0 | — | 2 |
| | Total | 62 | 27 | 34 | 95 | 75 | 15 | 35 | 31 | 41 | 74 | 0 | 2 | 42 | 55 | — | 588 |
| 1 | *Syracosphaera* | 13 | 19 | 0 | 0 | 12 | 39 | 31 | 0 | 19 | 28 | 29 | 0 | 0 | 34 | 53 | 277 |
| 2 | | 36 | 41 | 0 | 22 | 26 | 0 | 1 | 38 | 36 | 10 | 27 | 0 | 34 | 0 | 0 | 271 |
| 3 | | 26 | 20 | 0 | 0 | 19 | 30 | 45 | 0 | 32 | 50 | 0 | 39 | 0 | 37 | 58 | 356 |
| 4 | | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 30 | 0 | 1 | 27 | 0 | 19 | 0 | 0 | 88 |
| 5 | | 0 | 0 | 1 | 0 | 0 | 33 | 0 | 0 | 23 | 13 | 0 | 0 | 0 | 0 | 0 | 70 |
| 6 | | 45 | 23 | 0 | D. | 0 | 0 | 0 | 6 | 24 | 15 | 0 | 0 | D. | 33 | 40 | 186 |
| 7 | | 0 | 10 | 0 | — | 0 | 33 | 0 | 1 | 0 | 0 | 0 | 1 | — | 0 | 0 | 45 |
| | Total | 120 | 113 | 12 | 22 | 57 | 135 | 77 | 75 | 134 | 117 | 83 | 40 | 53 | 104 | 151 | 1293 |
| 1 | *Ditylum* | 23 | 0 | 27 | 24 | 24 | 19* | 3 | 51 | 23 | 28 | 26* | 12 | 23 | 19 | 26 | 328 |
| 2 | | 36 | 0 | 31 | 32 | 23 | 30* | 10 | 0 | 23 | 2 | 26* | 42 | 32 | 34 | 8 | 329 |
| 3 | | 15 | 0 | 20 | 43 | 0 | 29* | 1 | 21 | 34 | 41 | 29* | 25 | 23 | 26 | 40 | 347 |
| 4 | | 33 | 7 | 0 | 0 | 0 | K. | 0 | 0 | 22 | 31 | 0* | 0 | 0 | 16 | 0 | 109 |
| 5 | | 27 | 0 | 23 | 21 | 19 | — | M. | 1 | 2 | 16 | 14* | 0 | 18 | 21 | 19 | 181 |
| 6 | | 22 | 34 | 18 | 37 | 23 | — | 7 | 42 | 50 | 27 | 12* | 16 | 14 | 35 | 29 | 366 |
| 7 | | 2 | 6 | 7 | 7 | 1 | — | M. | 39 | 1 | 6 | 14* | 4 | 0 | 2 | 1 | 90 |
| | Total | 158 | 47 | 126 | 164 | 90 | 78 | 21 | 154 | 155 | 151 | 121 | 99 | 110 | 163 | 123 | 1750 |
| 1 | Starved | 32 | 50 | 26 | 43 | 38 | 43 | 11 | 8 | — | — | — | — | — | — | — | 251 |
| 2 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28 | — | — | — | — | — | — | — | 28 |
| 3 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | — | — | — | — | — | 0 |
| 4 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | — | — | — | — | — | 0 |
| 5 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | — | — | — | — | — | — | — | 0 |
| 6 | | 0 | D. | 3 | 0 | 0 | 0 | D. | 0 | — | — | — | — | — | — | — | 3 |
| 7 | | 0 | — | 0 | 0 | 3 | 0 | — | 0 | — | — | — | — | — | — | — | 3 |
| | Total | 32 | 50 | 29 | 43 | 41 | 43 | 11 | 36 | — | — | — | — | — | — | — | 285 |

* *helgolandicus*. M. = moribund; D. = dead; K. = killed.

Table VI shows the summarized results of all feeding experiments.

In a culture of *Chlorella* as rich as the *Chlamydomonas* used, the egg production was extremely low, even lower than in the starved. The faecal pellets

## TABLE VI. COMPARISON OF THE EFFECT OF DIFFERENT FOODS ON EGG PRODUCTION

| | | | Total no. of eggs laid on day | | | | | | | Omitting first day | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date begun | No. of *Calanus* | Food | 1 | 2 | 3 | 4 | 5 | 6 | 7 | No. laying | Total no. of eggs | Eggs per batch* | Eggs per *Calanus* per day |
| 29. i. 51 | 11 | *Chlamydomonas* | 49 | 28 | 140 | 76 | 157 | — | — | 9 | 401 | 20·4 | 9·1 |
| | 8 | Starved | 146 | 4 | 0 | 17 | 9 | — | — | 3 | 30 | 12·5 | 0·9 |
| 21. ii. 51 | 20 | *Chlamydomonas* | 245 | 66 | 189 | 203 | 304 | 77 | — | 18 | 839 | 21·4 | 8·8 |
| | 20 | Starved | 266 | 32 | 17 | 15 | 0 | 0 | — | 6 | 64 | 12·4 | 0·8 |
| 27. ii. 51 | 15 | *Chlamydomonas* | 312 | 174 | 375 | 214 | 177 | 105 | 138 | 14 | 1183 | 23·0 | 15·4 |
| | 15 | *Coscinodiscus* | 258 | 17 | 74 | 35 | 26 | 53 | 56 | 13 | 261 | 11·5 | 3·0 |
| | 15 | *Skeletonema* | 217 | 142 | 177 | 97 | 231 | 113 | 27 | 14 | 787 | 19·5 | 9·4 |
| | 15 | Starved | 236 | 32 | 3 | 0 | 11 | 31 | 7 | 9 | 84 | 8·9 | 1·0 |
| 6. iii. 51 | 15 | *Chlamydomonas* | 169† | 406 | 358 | 230 | 70 | 82 | — | 14 | 1146 | 29·0 | 16·4 |
| | 15 | *Peridinium* | 331† | 132 | 313 | 86 | 213 | 111 | — | 15 | 865 | 24·8 | 11·5 |
| | 15 | *Rhizosolenia* | 514 | 195 | 98 | 51 | 69 | 50 | — | 12 | 463 | 22·6 | 6·6 |
| | 8 | Starved | 63† | 49 | 32 | 0 | 0 | 1 | — | 5 | 81 | 15·4 | 2·3 |
| 12. iii. 51 | 15 | *Chlamydomonas* | 581 | 204 | 555 | 309 | 279 | 142 | 77 | 15 | 1566 | 30·5 | 17·4 |
| | 15 | *Dicrateria* | 547 | 16 | 1 | 102 | 37 | 26 | 18 | 11 | 200 | 16·8 | 2·5 |
| | 15 | *Chlorella* | 639 | 63 | 1 | 0 | 0 | 5 | 2 | 7 | 71 | 15·3 | 0·8 |
| | 15 | Indian Ink | 359 | 48 | 38 | 42 | 4 | 14 | 12 | 11 | 158 | 16·3 | 1·8 |
| | 8 | Starved | 208 | 50 | 3 | 2 | 28 | 0 | 22 | 6 | 105 | 19·8 | 2·2 |
| 22. iii. 51 | 15 | *Chlamydomonas* | 356 | 140 | 379 | 199 | 172 | 184 | 65 | 15 | 1139 | 26·6 | 12·8 |
| | 13 | *Hemiselmis* | 455 | 6 | 15 | 20 | 74 | 16 | 2 | 10 | 133 | 14·5 | 1·7 |
| | 15 | *Syracosphaera* | 277 | 271 | 356 | 88 | 70 | 186 | 45 | 15 | 1016 | 28·9 | 11·8 |
| | 15 | *Ditylum* | 328 | 329 | 347 | 109 | 181 | 366 | 90 | 15 | 1422 | 24·2 | 16·7 |
| | 8 | Starved | 251 | 28 | 0 | 0 | 0 | 3 | 3 | 2 | 34 | 28·0 | 0·8 |
| 23. iv. 51 | 13 | *Chlamydomonas* | 311 | 479 | 310 | 204 | 337 | 141 | 78 | 13 | 1549 | 32·1 | 20·7 |
| | 15 | *Lauderia* | 581 | 477 | 103 | 105 | 207 | 437 | 450 | 15 | 1779 | 33·4 | 21·2 |
| | 15 | *Gymnodinium* | 417 | 224 | 346 | 224 | 256 | 540 | 384 | 15 | 1974 | 29·9 | 21·9 |
| | 11 | Starved | 209 | 35 | 59 | 32 | 39 | 0 | 17 | 7 | 182 | 16·2 | 2·8 |

* Numbers below 5 omitted.

† Those of *Chlamydomonas* and 'starved' and three of those with *Peridinium* had been in the laboratory overnight and had probably laid their first batch of eggs.

consisted of a mass of *Chlorella* cells apparently unchanged. *Dicrateria* and, as already mentioned, *Hemiselmis* were both used but neither was a good food. The coccolithophore *Syracosphaera* was readily taken and egg production was high. This was true also of the dinoflagellate *Peridinium trochoideum*. The five diatom species used all gave a positive result, although some were apparently better than others. Production in *Coscinodiscus*, for instance, was only a little higher than in the starved, but the cells were large and lay almost entirely on the bottom of the dish where they may not have been so readily available. Only *Peridinium trochoideum*, *Gymnodinium*, *Syracosphaera*, *Ditylum* and *Lauderia* were as good as *Chlamydomonas*, although *Skeletonema* (whose cells were mostly on the bottom) was nearly as good.

One inert substance was used, a very dilute suspension of Indian ink. With this the *Calanus* produced faeces, but the egg production was no higher than in the starved. Thus egg-laying is not caused by the mere passage of material through the gut. In order to test whether the high pH value or some other factor accompanying a phytoplankton increase had any effect, female *Calanus* were kept in sea water whose pH value had been raised to about 8·2, and also in sea water to which cell-free filtrate from a rich *Chlamydomonas* culture had been added. Neither showed any effect on egg production.

The results show that even although they may be freely taken into the gut, not all the organisms available in the sea are of equal value for egg production. If, as seems probable, the food taken is used in the formation of the eggs laid, then its metabolism must be very rapid. The experiments suggest that egg production by ripe *Calanus* can be used to test the nutritive value of different food organisms. It is a simpler and quicker method than feeding copepodites through one or more moults, during which development may also be affected by factors other than food.

An attempt was made to measure the relation between increase in food and increase in egg production. The *Calanus* were kept in *Chlamydomonas* cultures varying in concentration from 0 to about 250 cells/mm.$^3$ and the medium changed every other day. The results are shown in Table VII and Text-figs. 3 and 4. With concentrations as low as 7–8 cells/mm.$^3$, the egg production is practically the same as with the starved *Calanus*. It then increases rapidly with increase in food up to about 40 cells/mm.$^3$, after which the curve flattens off. Although in the richer concentrations some of the *Chlamydomonas* cells sank to the bottom and were thus less available, it may be concluded that beyond a certain point more food will not lead to greater egg production. If a *Chlamydomonas* cell is considered to be of equal food value to a *Skeletonema* cell (being of about equal size), the lowest figures which gave an increase in egg production are less than those of a normal spring diatom increase in the Clyde sea area.

Some experiments in the spring of 1950 had suggested that the presence of food might act as a trigger to set off egg-laying. This was not confirmed in

## TABLE VII. EFFECT ON EGG PRODUCTION OF FEEDING WITH INCREASING CONCENTRATION OF CULTURE. 3–10 MAY 1951

| | | Total no. of eggs laid per *Calanus* up to day | | | | | | Omitting first day | | |
|---|---|---|---|---|---|---|---|---|---|---|
| No. of *Calanus* | Strength of culture (cells/mm.$^3$) | 2 | 3 | 4 | 5 | 6 | 7 | No. laying | No. of eggs per batch* | Eggs per *Calanus* per day |
| 15 | 200–250 | 38·3 | 74·2 | 95·7 | 108·5 | 117·0 | 119·4 | 14 | 34·0 | 21·2 |
| 15 | 70–80 | 38·7 | 61·9 | 83·5 | 93·1 | 98·9 | 106·5 | 15 | 29·5 | 18·7 |
| 15 | 34–40 | 36·0 | 61·5 | 71·2 | 82·4 | 87·1 | 88·7 | 14 | 32·2 | 15·1 |
| 15 | 14–16 | 23·5 | 31·4 | 37·8 | 39·5 | 40·8 | 42·2 | 15 | 25·0 | 7·2 |
| 15 | 7–8 | 13·9 | 19·8 | 21·7 | 24·1 | 25·9 | 26·4 | 15 | 18·5 | 4·6 |
| 15 | 0 | 12·9 | 19·6 | 19·7 | 21·4 | 21·4 | 21·5 | 10 | 28·2 | 3·6 |

* Numbers below 5 omitted.

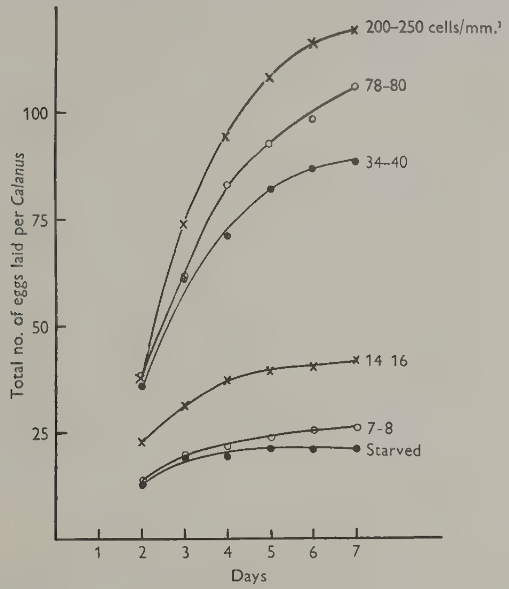
## TABLE IX. EGG PRODUCTION OF RIPE FEMALES KEPT IN UNFILTERED SEA WATER, 1951

| | | Total no. of eggs laid on day | | | | | | | Omitting first day | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date begun | No. of *Calanus* | 1 | 2 | 3 | 4 | 5 | 6 | 7 | No. laying | Total no. | Eggs per batch* | Eggs per *Calanus* per day |
| 21. ii. 51 | 20 | 270 | 7 | 2 | 33 | 20 | 7 | — | 7 | 69 | 20·0 | 0·7 |
| 27. ii. 51 | 15 | 273 | 14 | 1 | 0 | 0 | 8 | 0 | 8 | 23 | 8·0 | 0·3 |
| 6. iii. 51 | 15 | 366 | 156 | 63 | 31 | 10 | 5 | — | 14 | 265 | 20·6 | 3·6 |
| 12. iii. 51 | 15 | 499 | 31 | 82 | 25 | 12 | 8 | 25 | 9 | 183 | 17·8 | 2·2 |
| 22. iii. 51 | 13 | 367 | 1 | 19 | 0 | 44 | 11 | 3 | 5 | 78 | 18·5 | 1·1 |
| 23. iv. 51 | 15 | 512 | 77 | 62 | 160 | 44 | 66 | 72 | 14 | 481 | 17·7 | 5·7 |
| 3. v. 51: | | | | | | | | | | | | |
| 1st week | 14 | 681 | 156 | 552 | 214 | 187 | 138 | 111 | 14 | 1358 | 31·3 | 16·2 |
| 2nd week | 14 | 61 | 84 | 274 | 317 | 259 | 91 | 194 | 13 | 1280 | 24·7 | 13·9 |
| 3rd week | 11 | 117 | 82 | 157 | 27 | 51 | 25 | 47 | 10 | 506 | 25·5 | 6·9 |
| Three weeks | — | — | — | — | — | — | — | — | — | 3144 | 27·4 | 12·6 |

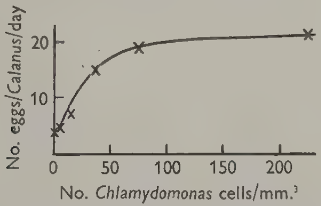
* Numbers below 5 omitted.

In the experiment beginning on 3 May the first day is not omitted in the calculations for the second and third week.

1951: the shock of capture and examination seems to be enough. The presence or absence of food has no effect on the number of eggs or the number of females laying immediately after capture.



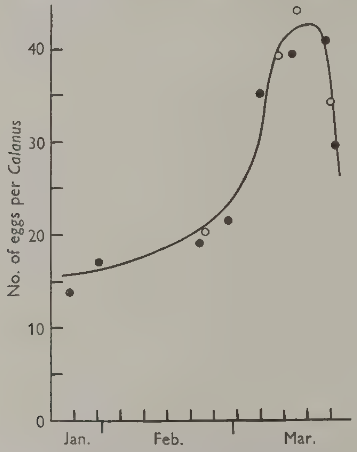
Text-fig. 3. Effect on egg production of feeding *Calanus* on *Chlamydomonas* cultures of different concentrations.



Text-fig. 4. Average number of eggs laid per day by *Calanus* fed on *Chlamydomonas* cultures of different concentrations.

The average number of eggs laid by a 'ripe' *Calanus* on the first night after being brought into the laboratory increased from January to March, as is shown in Text-fig. 5 and Table VIII. The increase was at first slow, but in both 1950 and 1951 there was a steep rise in March and a subsequent fall. In 1950 the maximum number (44·4) on 14 March can be related to a normal increase of *Skeletonema*, which by then had reached a figure of 340 cells/ml.

In 1951 the maximum egg number (41) was not quite so high and corresponded to a much smaller increase of *Chaetoceros* and *Coscinodiscus*. After this the number laid per batch fell and it is possible that this is because the females were now laying in the sea. *Calanus* eggs were scarce in the sea on 2 March, there were a few on 14 March and considerable numbers were present on 20 March. The results suggest that until the middle of March the female is enlarging the eggs gradually but not necessarily laying them in the sea.



Text-fig. 5. Number of eggs per batch produced by *Calanus* during the spring. ○, 1950; ●, 1951.

TABLE VIII. AVERAGE NUMBER OF EGGS IN FIRST LAY OF RIPE *CALANUS*

(Numbers under 5 omitted.)

| Date | No. of *Calanus* | Average no. of eggs | Date | No. of *Calanus* | Average no. of eggs |
|---|---|---|---|---|---|
| 22. ii. 50 | 5 | 20·4 | 21. ii. 51 | 41 | 19·0 |
| 10. iii. 50 | 25 | 39·2 | 27. ii. 51 | 60 | 21·4 |
| 14. iii. 50 | 46 | 44·1 | 6. iii. 51 | 29 | 35·2 |
| 21. iii. 50 | 16 | 34·3 | 13. iii. 51 | 69 | 39·4 |
| 24. i. 51 | 7 | 13·9 | 20. iii. 51 | 94 | 41·0 |
| 30. i. 51 | 11 | 17·1 | 22. iii. 51 | 69 | 29·6 |

When the first generation reaches maturity the average number of eggs per batch rises again, and on 30 April–1 May was 64·2.

During the experiments on different foods a number of ripe females was also kept in unfiltered sea water in the hope of finding out whether the sea during the spring diatom increase would become a medium as effective as the cultures used. Unfortunately the spring of 1951 was quite abnormal, and the enormous numbers of *Skeletonema* which usually appear in March did not come until May. Instead there was about the middle of March a much smaller increase in the numbers of *Chaetoceros* and *Coscinodiscus* and this was apparently sufficient to let the breeding of *Calanus* go on as usual.

In the laboratory the number of eggs laid in sea water (Table IX) was very low in February, rose a little in March and April but did not equal the cultures used until the first-generation females were laying during the *Skeletonema* increase in May. Until May the low numbers may have been caused partly by the small volume in which the *Calanus* were kept — 20 ml. changed every second day. Gauld (1951) has shown that a Stage V *Calanus* can filter an average of about 70 ml. per day.

In May, therefore, fourteen *Calanus* were kept each in 50 ml. of water which was changed daily, and in the 21 days during which they were kept the egg production per *Calanus* varied from 187 to 422. Towards the end of the 3 weeks egg production fell off considerably, although diatoms were still numerous in the sea water. In spite of this the females when examined on the 21st day mostly contained a number of large eggs apparently ready to lay. One of them is shown in Pl. I c. The egg production per *Calanus* per day was 16·2 for the first week and 12·6 for the whole time, thus approaching the production by *Calanus* kept in *Chlamydomonas* culture.

The high egg production in these females (nine of the 11 surviving laid over 250 eggs in the 21 days) shows that the figures given for the spermatophore-bearing females (Text-fig. 1) may well be equalled or exceeded by *Calanus* in the sea.

## DISCUSSION

It is interesting to consider the relation of these results to events in the sea.

When the over-wintering stock of Stage V comes to moult in the beginning of the year it does so with a good store of fat, in spite of having spent several months in diatom-poor water. It may be that the *Calanus* can find more food in winter than is supposed, or that its metabolism in winter is lower than during the rest of the year. That a lowered metabolism in winter may be an important factor is indicated by the results of several experiments comparing the food taken in by Stage V and female *Calanus* in the same culture of *Chlamydomonas*. On 10 January, judging from the number of faecal pellets produced, the Stage V were eating less than half the amount that the females were. The experiment was repeated with the same results on 23 January and on 13 March; by 9 April, however, the new generation had appeared and Stage V was eating as much as, or more than, the females.

In 1950 the over-wintering Stage V *Calanus* began to moult in the end of December, and by the middle of February 1951 most of the population consisted of adult females. On 1 February 53 % of the females were immature and only 4 % ripe, but the proportion of ripe increased gradually until on 5 March 1 % was immature and 94 % were ripe. *Calanus* eggs were scarce in the sea on 2 March, but considerable numbers of both eggs and nauplii were present on 20 March and the new generation grew up during the rest of March and April. Adult females of the new brood appeared on 12 April as immature and gradually replaced the over-wintering stock.

Nicholls (1933*a*) estimated from field work that a female after moulting takes about a month before the eggs are ready to lay. The egg-laying experiments, however, have shown that the time taken will depend very much on the food present in the sea. When given a plentiful supply an 'immature' female can lay eggs in 4 or 5 days and a 'semi-ripe' one in 2 or 3, but the experiments with the females carrying spermatophores indicate that they do not often lay within a week after fertilization. The time taken from moulting up to this stage is uncertain and must depend partly on the stage of maturity at moult. The results with very immature females (p. 529) indicate a lapse of 2–3 weeks, but the fact that the proportion of immature females found in tow-nettings is low makes it more likely that the time is usually shorter. The fluctuating food conditions in the sea make it certain that the period from moulting to maturity will be longer than in the laboratory, and the dates given above for the increase in ripe females from 4 to 94 % confirm Nicholls's estimate of about a month. The experiments also indicate that the life of a female may be considerably longer than has been hitherto supposed, for besides the 4 weeks or so taken to mature it may live at least another month laying successive batches of eggs.

The facts that the number of enlarging eggs in the female (judging from the numbers laid per batch) increases over a period of some weeks, and that during that time the eggs are scarce in the plankton indicate that the female does not need to lay eggs once they have matured but can retain them until the conditions are favourable. Unless food is present *Calanus* will lay only a few eggs in the sea; a large egg production will occur only with a diatom increase lasting some time. The actual stimulus to egg-laying and to the completion of the first maturation division which immediately precedes it is unknown. Food does not act as the immediate stimulus, but when available it seems to be rapidly digested and used for egg production.

The production of viable eggs after as much as 68 days by an isolated female *Calanus* is interesting in that it shows that a single fertilization is sufficient. In the sea males reach their peak of abundance before females and the percentage of females bearing spermatophores is highest early in the development of a generation. Only on rare occasions do the majority of females bear spermatophores. This is understandable when we remember that the spermatophore is carried for only 1 or 2 days, after which it drops off. When females are caught in the sea they are almost invariably fertilized, that is, the spermathecae are dark in colour and full of sperm. A few females were found with empty spermathecae, and some of these were kept in a dish with males but fertilization did not take place. Males do not live in captivity so well as females and copulation was never seen.

The maximum total number of eggs laid by a single female (586) is much above the only previous estimate, over 112, which is that of Raymont & Gross (1942). However, their *Calanus* may have laid before their observations began.

Not all feeding experiments resulted in egg production. With the possible exception of *Coscinodiscus* all the diatoms tried gave positive results. Other organisms were also successful, but perhaps more surprising is the complete failure of *Hemiselmis* and *Chlorella*. *Chlorella* is known to be difficult to attack because of its cellulose membrane, but on the same grounds it might have been expected that *Chlamydomonas*, which in fact gave very good results, would be difficult to digest. Raymont & Gross (1942) found that *Nitzschia closterium* var. *minutissima* and *Chaetoceros pseudocrinitus* as well as several flagellates were eaten, although the *Calanus* survived better with the diatoms. The present observations extend and amplify their findings.

Nicholls (1933*b*) suggested that *Calanus* spawns at night, since eggs and young stages are always found above 30 m., and this has now been confirmed for the over-wintering generation. The eggs are heavier than sea water, and the rate of sinking is given by Gross & Raymont (1942) as 36 m. in 24 hr. Since the minimum time of hatching is about 24 hr. the greatest depth at which the eggs will be found should be about 36 m. In the results of Nicholls (1933*a*) and of Marshall *et al.* (1934) the vertical hauls were divided at 30 and 10 m. respectively. When summed over the year the number of nauplii above and below 10 m. was approximately the same, but very few were found below 30 m. The young copepodites do not show diurnal vertical migration (Nicholls, 1933*b*) and are confined to the surface layer so that the nauplii must swim up towards the surface. Since females show a marked diurnal vertical migration, the fact that the eggs are laid during the night ensures that they will be laid fairly near the surface. The first generation, which becomes adult towards the end of April and in May, is found near the surface during the day and lays throughout the 24 hr. However, those females of the first generation which live in deep water also lay throughout the 24 hr., and this is more difficult to understand. For if nauplii hatch below 50 m. they will have a much longer way to swim up to the surface layers.

The suggestion that successive broods of *Calanus* depend on outbursts of diatom growth is supported by the evidence given here of the dependence of egg-laying on food. Although the experimental results show that food and egg-laying are closely connected, it does not follow that a food which will induce egg-laying will also be suitable for the feeding and development of the nauplii and early copepodite stages. Some preliminary work has shown, however, that even as large a diatom as *Coscinodiscus centralis* can be broken up and ingested by Copepodite Stage II, and that *Peridinium trochoideum* ($25 \times 19\,\mu$) can be eaten by at least Nauplius VI.

The production of broods by some of the smaller copepods also seems to depend on diatom outbursts (Marshall, 1949), and it may therefore be expected that these will show a similar effect of feeding on egg-laying.

We have pleasure in acknowledging the help given throughout the work by the staff of the Marine Station. We are very grateful to Dr Mary Parke of the Plymouth Laboratory for sending us cultures of all the organisms used.

## SUMMARY

A description is given of female *Calanus* at different stages of maturity and of the process of egg-laying.

It has been observed that the eggs of the two forms of *Calanus* differ in size, those of *helgolandicus* being larger than those of *finmarchicus*. The former was scarce, about 4 %, in the over-wintering stock.

The females of the over-wintering stock of *Calanus* lay their eggs early in the morning, mainly between midnight and 3 a.m.; those of the first generation, which come to maturity in May, lay throughout the 24 hr.

The total egg production of individual females kept in the laboratory and fed has been found. The maximum was 586 eggs. Egg-laying may be spread over as much as 74 days and tends to occur in a series of bursts, each burst lasting for about a week. A single fertilization is enough for the whole of the egg-laying.

Egg production is largely dependent on the food available. When females are starved egg-laying ceases, but if they are fed again egg production begins too and is eventually not much less than in *Calanus* fed continuously.

A number of different cultures of diatoms and flagellates were tested as food, but it was found that not all of them resulted in egg production. All diatoms tested were successful. Inorganic material or a change in the reaction of the medium had no effect on egg production.

*Calanus* when kept in natural sea water produced only small numbers of eggs unless the water was rich in diatoms.

When brought into the laboratory ripe *Calanus* usually lay eggs overnight. The number thus laid was low in January and February and increased rapidly in March to a maximum of about 40 per batch. With the first-generation females much higher numbers were obtained.

The relation of these results to events in the sea is discussed. It is suggested that even when ripe a female *Calanus* can defer egg-laying until a suitable food supply is available. The spawning of *Calanus* in the sea should therefore coincide with diatom increases.

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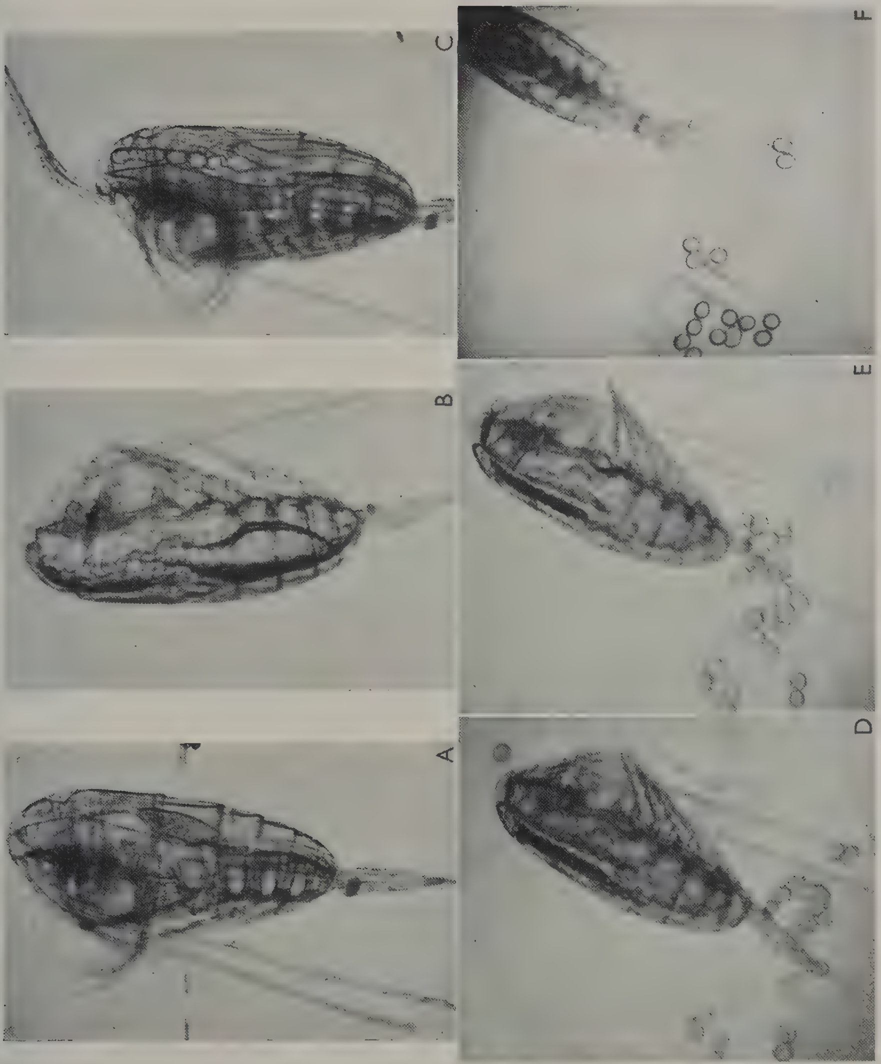
## EXPLANATION OF PLATE I

A. Female *Calanus* with ovary in medium state. The diverticula from the genital ducts fill only part of the head end. B. Female *Calanus* with ovary in ripe state. Large eggs are seen filling the diverticula in the head end and along the course of the oviducts. C. Female *Calanus* with ovary in ripe state. This *Calanus* has already laid many eggs and they are not so crowded as in B, but one row of large eggs is visible. D. *Calanus* in the process of laying eggs which have not yet begun to round off. E. The same *Calanus* slightly later. The same groups of eggs can be traced and the earlier laid are rounding off. F. A later stage in egg-laying. Some of the eggs are now spherical.



Figs. A–F.

# CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L.

## III. AGE AND GROWTH

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(Plate I and Text-figs. 1–4)

## Introduction

The first serious attempt to determine the age and growth rate of the common mackerel (*Scomber scombrus* L.) appears to have been made by Captain Atwood in 1856 (quoted by Brown Goode, 1884, p. 116) in the Massachusetts Bay area of northern North America. Small fish caught by Atwood in October of that year measuring 6½–7 in. in length (16·5–17·5 cm.) he believed to be the young of the year (i.e. they belonged to the O-group). Mackerel belonging to this group he calls 'spikes'. 'Blinks', 'tinkers' and 'second size' fish he assigns to the I-, II- and III-year age groups respectively, but unfortunately gives no data as to the sizes of those categories, merely stating that everyone well acquainted with mackerel makes the same groupings 'as there seems to be a line of demarkation between the different kinds which stands out prominently'. Sixteen years later, on 27 July 1872, Malm (1877, p. 409) observed large numbers of small mackerel close inshore in the Gullmarfjord near Christineberg. Several tons of those mackerel were enclosed in a seine, but only ten specimens were retained as all the others escaped through the meshes. These ten fish ranged in length from 67 to 100 mm. and Malm surmised their age to be 13 months. Collett (1880, p. 18) stated that on the coast of Norway 1-year-old mackerel are 'fingerlang'. To fish of 20 cm., taken at the end of August, he ascribed (without supporting data) an age of 2 years, with sexual maturity supervening at 3 years at an unspecified length. Marion (1889, p. 86) studied the same species of mackerel in the Mediterranean. In catches obtained at Nice between 2 and 9 May 1888 he found small individuals from 6 to 11 cm. in length, which he considered to be derived from eggs spawned during the preceding January to March, the range of size being attributed to a spread of spawning activity over those 3 months. In the Gulf of Marseilles, too, at the end of May, Marion obtained mackerel of 11 cm. which he considered to be the young of the year. At the end of the year fish of 15–18 cm. were common. Still later, at the beginning of February, both at Marseilles and farther west, Marion noted the presence of mackerel measuring 20–24 cm.

These he considered to be derived from the previous year's spawning—i.e. they were the survivors of the brood that in May, 9 months earlier, were 6–11 cm. long.

Along the shores of the Mediterranean mixed fish fry is a readily marketable commodity which commonly includes mackerel. On certain dates in 1891 Gourret (1891, p. 57) recorded the following quantities and sizes landed by a small shore fishery near Marseilles:

| | kg. | cm. |
|---|---|---|
| 17–23 April | 70 | 4–8·5 |
| 10–13 May | 30 | 2–3 |
| 11, 12, 14, 17 May | 31 | 3–4 |
| 23, 26 May | 6 | 3–5 |
| 29, 31 May | 25 | 3–6 |

The April fry Gourret believed to be derived from the earliest spawning of that year, perhaps in January. The various May fry he ascribed to spawning in February (5–6 cm.); March (4–5 cm.) and even April (2–3 cm.).

In 1892 (pp. 232–3) and again in 1896 (p. 314) Cunningham expressed the belief that mackerel of from 22·2 to 23·5 cm. in length, caught on 10 June, must be more or less exactly 1 year old. Others taken on 23 June having a length range of 29·5–32·8 cm. he regarded as precisely 2 years old. Still others of 16–21 cm., taken in November, were assumed to be 16 months old. This discrepancy Cunningham attributed to individual variation in size, but was greatly perplexed by a single specimen of 13·8 cm. taken in September 'which could not have reached that length in 2 or 3 months and must have been an unusually small specimen at 14 months'. Cunningham's age estimations were based on the erroneous belief that in all the mackerel of the region spawning is 'approximately simultaneous', proceeds very rapidly when once begun, and is limited definitely to one short period of the year extending from about the beginning of June to mid-July (Cunningham, 1889, p. 25; 1896, p. 313: cf. Steven, 1949, p. 565).

Matthias Dunn (1893, pp. 4–5) expressed the firm opinion that in the western end of the English Channel young mackerel 5–6 in. long (12·7–15·2 cm.) at the end of August, are derived from that year's spring spawning. According to Dunn, these small fish stayed inshore for a further 2 months or so, growing meanwhile at the rate of about 1¼ in. (3·2 cm.) per month. By about the end of October when 7½–8½ in. long (19–21·6 cm.) they disappeared from Dunn's ken until about the beginning of the following June, by which time they had attained a length of from 9 to 11 in. (22·9–27·9 cm.). Ehrenbaum (1923, p. 21) records that Knut Dahl caught 311 specimens of small mackerel ranging in length from 6 to 9 cm. in a seine net on 19 July 1905. This total was made up as follows:

| Length (cm.) | 6 | 7 | 8 | 9 | (mean 7·8) |
|---|---|---|---|---|---|
| No. of fish | 5 | 102 | 162 | 42 | |

Ehrenbaum considers all these fish to have been in their first year of life. Young mackerel of similar sizes have also been taken in small numbers, by other observers elsewhere from time to time without their ages having been determined or surmised. These various records are collected by Ehrenbaum (1923, pp. 12–26), who reaches the conclusion that, in general, the growth of the mackerel (*Scomber scombrus*) during the first year of life 'does not seem to amount to much over 10 cm.' (p. 22). Towards the end of their second summer Ehrenbaum considers the average length to be 20–22 cm., and 27–28 cm. in the third summer (p. 39).

Nilsson (1914, pp. 1–59) was the first investigator to make any real attempt to determine the age and growth rate of mackerel after the first year of life. Age determination in this fish is a matter of great difficulty. No bone has been found which reveals distinctive growth markings either with or without special treatment. Visible and readable markings are present on certain scales, but there is great difficulty in collecting them. They are so small as to be easily rubbed off and transferred from one fish to another in all samples collected by ordinary methods. For scales to be used reliably mackerel must be caught individually, e.g. by hook and line, and each fish kept by itself in a separate container—conditions that cannot easily be met if adequate numbers are to be dealt with. Otoliths are less clearly marked, but with practice readings can be obtained from a high proportion of them in the younger year classes—up to about 6 years. In my experience otoliths from older fish are seldom readable.

Nilsson (1914, p. 20) used scale readings checked against a few otolith determinations for age assessment of 208 specimens. From this somewhat scanty material he gives the following lengths reached by mackerel at the end of each year of growth up to and including 6-year-old fish (lengths measured to tip of tail):

| | | |
|---|---|---|
| End of 1 year | Maximum recorded length | 22·9 cm. |
| „ 2 years | 23·5–30·6 cm. | |
| „ 3 years | 31·1–33·9 cm. | |
| „ 4 years | 34·4–36·1 cm. | |
| „ 5 years | 36·7–38·5 cm. | |
| „ 6 years | 39·1–40·3 cm. | |
| „ 7 years | 40·9–? | |

Nilsson's findings are in agreement, therefore, with those who ascribe to the mackerel a growth of 20 cm. or more in the first year of life, as against those who consider fish of this size to be at or near the end of their second year of life.

This divergence of opinion as to the growth rate of the mackerel, at any rate in its early years, has persisted. As late as 1939 Le Gall (p. 14) gives the following figures based on length frequencies (not given) and the distribution throughout the year of mackerel shoals comprising fish of different sizes.

| | |
|---|---|
| End of 1 year | 8–11 cm. |
| „ 2 years | 18–21 cm. |
| „ 3 years | 26–28 cm. |
| „ 4 years | 30–32 cm. |
| „ 5 years | 35 cm. |

At the same time, Steven and Corbin (1939, p. 18) made considerably different tentative assessments of age and growth rate based on scale and otolith readings. These were:

| | |
|---|---|
| End of 1 year | ? |
| „ 2 years | Up to 27 cm. |
| „ 3 years | „ 31·5 cm. |
| „ 4 years | „ 33·5 cm. |
| „ 5 years | „ 35·0 cm. |
| „ 6 years | „ 35·5 cm. |
| „ 7 years | „ 36·0 cm. |

According to Sette (1943, p. 154), on the American side of the North Atlantic the fry of the common mackerel reach a length of about 50 mm. in about 70 days after hatching—i.e. by about the end of July for the majority of them. Subsequently, Sette (1950, p. 312) states, without supporting data, that these July fingerlings reach a length of 8 in. (i.e. just over 20 cm.) by September; and that they range, in their second year of life, from 25 cm. in early summer to 32 cm. by fall.

Recently, Le Gall (1950) has repeated his 1938 figures concerning age and growth of mackerel, again without supporting data, but with the accompanying remark that 'la présence, en quantités parfois très abondantes de la mi-Juin à la fin de Septembre, de jeunes maqueraux de 7 à 11 centimètres, confirment l'opinion que nous avons deja émise sur la croissance de ce poisson'.

The two schools of thought on mackerel growth are at variance mainly in their conclusions concerning rate of growth in the first year of life, one school placing the first year's increment at 10 cm., or a little over, while the second attributes a length of 20 cm. or more at the end of the first year. Ehrenbaum, of the first school, supports his view by saying that the mackerel is hardly likely to grow faster than cod and haddock, which at the end of their first summer measure only about 14 cm. (1923, p. 23).

Striking confirmation of rapid growth by mackerel in their first year of life has recently been provided by Dannevig (1947, p. 93; 1948, p. 219), who has been able to make direct observations on the growth of young mackerel in his fish-hatchery basins at Flødevigen, Norway. On 6 August 1939, a number of young mackerel, 8 cm. in length, appeared in the leads between the basins and the lobster hatchery. One was caught and placed in an aquarium where there were large quantities of small Crustacea, and throve remarkably. Later it could be provided with only dead food which did not agree with it, and it died on 1 September being then 10·5 cm. long. The fish had grown 2·5 cm. in 25 days. Later, on 14 September, about twenty small mackerel were observed in the oyster basins. Their lengths were approximately 15 cm. The basins had been emptied in the spring and those small mackerel must have entered as eggs contained in the water pumped into the basin in May–June of the same year. Dannevig states that young fish could not have passed through the centrifugal pump and lived. He is therefore in no doubt that those mackerel were young fish of the current year and that they had reached a length of 15 cm. in about 4 months. This agrees closely with Dunn's figures of 12·7–15·2 cm. length at the end of August in the English Channel. There can be now no doubt that mackerel may reach a length of 20 cm. or more in the course of their first year of life.

## METHODS

Investigations by the present author into the life history and biology of mackerel in the English Channel and Celtic Sea have included researches into ages and growth rates. Otoliths have been collected from a total of 8422 fishes, of which 6261 (74·3%) have been readable and 2161 (25·7 %), mainly in the higher length groups, have been unreadable. In addition, scales from 1364 fish were collected, but scale reading was discontinued when it was found that a sufficient proportion of otoliths could be read to give reasonably satisfactory results.

The otoliths were collected from each fish by cutting transversely through the head behind the eye at a point immediately in front of the small cavities in which the otoliths lie. There are two otoliths on each side, but the smaller one is useless for age determination. After the cut is made the brain is removed from the remaining posterior part of the cranium. The large otoliths can then be removed, one at a time, by probing for them with a weakly-sprung sharp-pointed forceps. At first this may present some difficulty, but with a little practice the operation becomes both simple and speedy.

As thus obtained, each otolith is covered with soft tissues that must be completely removed before drying. This cannot conveniently be done immediately, as too much time would be taken up in disposing of the sample of fish. The otoliths are therefore stored under water until they can be cleaned. This is best done by making shallow holes in a block of hard, close-grained wood about 9 in. square. One hundred such holes, preferably $\frac{5}{8}$ in. in diameter and $\frac{3}{16}$ in. deep, can conveniently be made in such a block. They should be arranged in regular rows of 10 × 10. Above the uppermost hole in each vertical row the numerals 1–10 are clearly marked. The whole upper surface of the block, including the shallow holes, should then be painted black with a waterproof paint that will retain the water with which the holes have to be filled. A specially made block of black plastic material would be even more suitable. On removal from the fish the otoliths are placed in the appropriate hole which is filled with water to keep them wet.

As soon as possible after the sample has been dealt with the otoliths must be divested of all soft tissues adhering to them and placed in numbered containers. Envelopes are unsuitable as the otoliths are so small and brittle that they become lodged in the corners, are hard to see, and often get broken. The best method is to glue small cardboard pillboxes by their bottoms on a square piece of cardboard—100 boxes arranged in rows of 10 × 10 to each piece of board.

To clean the otoliths two pieces of cane about 3 mm. in diameter and 15 cm. long are used. Before use each piece is sharply pointed at one end and the points worked gently backwards and forwards on a piece of glass. This breaks up the single fine point and releases the fibres so that a tiny brush of just the right stiffness is formed. With two brushes thus prepared the otoliths can be easily and completely cleaned in water in a solid watch-glass, preferably of black glass, under the low power of a dissecting microscope.

Mackerel scales are very small and easily rubbed off. Special precautions had therefore to be taken to ensure that the scales removed from a fish really belonged to it. Nilsson's method of using hooked fish for scale-reading purposes was therefore adopted. Each fish, on removal from the water carefully suspended from its hook so as not to touch anything, was lowered tail first into a clean, grease-proof paper bag. Both bag and fish were then held firmly in the left hand while the hook was removed. By adopting this method, very few scales actually became dislodged from the fish, and any that were rubbed off were inside that fish's own bag.

For age determination, scales from the anterior part of the body just below and slightly behind the pectoral fin have invariably been used. A scraping in this position is made with a scalpel and the small mass of scales so collected is washed off into a small specimen tube ($1\frac{1}{2} \times \frac{1}{2}$ in.) almost filled with clean water. The tube is then corked. Groups of 100 tubes are used, fitted into a 10 × 10 arrangement of holes in a block of wood, the holes smaller and deeper than those made for the reception of otoliths.

The scales are collected and stored in tubes because they are too small to be removed individually with a pair of forceps, followed by dipping in water, cleaning between the thumb and first finger of the left hand, and mounting on a microscope slide—as can be done with herring and pilchard scales, for example. In their tubes they can be left for an indefinite period before eventual cleaning and mounting. If left for more than a few days the contents of the tube will smell strongly, but this does no harm; indeed it is an advantage because the scales are more easily cleaned after the organic matter covering them has decomposed. In a normal scraping anything up to 500 scales may be present. From amongst these at least three scales should be selected for mounting. In most samples, scales of many shapes and sizes will be found of which only a few will be readable. Most kinds are well illustrated by Nilsson (1914, plate I, figs. 1–13). The clearest and most consistent zoning and ringing are found on those shaped as in Nilsson's figs. 8 and 11. At least three scales of this type should be looked for amongst the mass of others, and removed to a second watch-glass. There they must be cleaned, in water, under a binocular dissecting microscope, using brushes made from pieces of cane in the way described above. Three such scales are shown in Pl. I, figs. 1–3.

## AGE AND GROWTH

In this investigation scales from each of 1364 fish were mounted on microscope slides previously smeared very lightly with prepared egg albumen. All these scales were separately 'read', and it was found that in 1343 out of the 1364 fish (98·5 %) the readings of all three scales were in agreement. In the remainder, the three scale readings did not all agree. This degree of discordance is not excessive and gives good grounds for assuming that the readings are reliable. Even more confidence can be placed in them when comparison is made with otolith readings from the same fishes. Omitting those fishes that gave discordant scale readings, it is found that in only fifteen out of a total of 1343 individuals (1·1 %) did the scale readings differ from those of the otoliths. Difficulty in reading the otoliths can very easily account for this discrepancy. These results are shown in detail in Table I.

In consequence of this satisfactory agreement between scale and otolith readings, the collection of scales was discontinued and only otoliths were taken from later samples. In this connexion it must be emphasized that a high proportion of otoliths were rejected as unreadable. Included in this group are all otoliths whose readings were to any appreciable extent doubtful. It is believed to be better to reject completely a doubtful reading than to include it in any group to which it 'probably' belongs.

In the mackerel there are two otoliths on each side—a larger and a smaller one. The latter, flat and somewhat irregularly crescent-shaped in outline, is generally almost completely transparent and never exhibits readable 'ringing' and 'zoning' (Nilsson, 1914, plate I, fig. 16). The larger otolith is thickest and widest at its posterior end, tapering towards its anterior end where it terminates in two points of unequal length. Nilsson (p. 23) states that this otolith 'can at times have fairly distinct annual rings, especially on the longer of the two points'. In the present investigations reliable readings have been more easily obtained at the blunt posterior end of the otolith.[1] While it is true that markings are often most distinct on the longer point, secondary markings are often so much in evidence that interpretation is difficult or impossible.

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[1] In Nilsson's own figures (plate I) the markings are clearest at the blunt ends of the otoliths shown.

Reading is best carried out in a solid watch-glass made of jet-black glass. The otoliths are viewed under water or alcohol by direct illumination.[1] Thus examined, the central part of the otolith shows up as opaque chalky white. In fish of more than 1 year the dense central portion is surrounded by a dark, narrow 'ring'. With increasing age further zones and rings are formed (see Pl. I, figs. 4–6).

TABLE I

| Serial no. of sample | Total fish | No. of fish with discordant scale readings | All scales in agreement but differing from otoliths | Percentage of fish with all scales and otoliths in agreement |
|---|---|---|---|---|
| *13A* | 100 | 6 | 1 | 93 |
| *15* | 61 | 4 | 1 | 92 |
| *24* | 96 | 0 | 0 | 100 |
| *29* | 93 | 0 | 0 | 100 |
| *31* | 71 | 0 | 5 | 93 |
| *32* | 99 | 0 | 0 | 100 |
| *37* | 13 | 0 | 2 | 85 |
| *39* | 49 | 0 | 0 | 100 |
| *41* | 100 | 10 | 1 | 89 |
| *44* | 20 | 0 | 0 | 100 |
| *45* | 40 | 0 | 0 | 100 |
| *46* | 50 | 0 | 0 | 100 |
| *47* | 41 | 0 | 0 | 100 |
| *48* | 39 | 0 | 0 | 100 |
| *49* | 51 | 0 | 0 | 100 |
| *50* | 40 | 0 | 0 | 100 |
| *52* | 58 | 0 | 1 | 98 |
| *54* | 45 | 0 | 0 | 100 |
| *55* | 48 | 0 | 2 | 96 |
| *56* | 50 | 0 | 0 | 100 |
| *57* | 100 | 0 | 2 | 98 |
| *58* | 100 | 1 | 0 | 99 |
| Total | 1364 | 21 | 15 | 97·4 |

The central zone is first laid down. This is followed by the first ring which, although formed in winter, does not generally become clearly defined until late spring or early summer when the new season's zone, now forming outside it, serves to show it up. This applies also to all the dark transparent winter rings that are laid down in subsequent years.

Unlike a ring, a zone is recognizable while growing, long before the next ring is laid down demarking its final limit. Thus a 2-zoned fish is one in which a fully developed central zone is surrounded by a fully formed ring, and a second zone, the latter being either partly formed or completed.

New zones, narrow and obviously of recent origin, begin to show up in late spring and early summer. Thus a fish in its second year, caught say in September, will have a distinct second zone clearly noticeable. Its otolith reading will therefore be '2 zones 1 ring', recorded as '2–1'. The same fish will continue to have a reading of '2–1' until next May or June when a third zone, newly forming, will show up the second winter ring. Readings of '1–1', '2–2', '3–3' have therefore seldom been made; for by the time that the new zone has shown up the immediately preceding winter ring clearly, it has become itself recognizable and must be recorded. It will be convenient, therefore, to discuss otolith readings in terms of zone numbers. An otolith with two zones will obviously have a winter ring between them; a three-zoned otolith will have two intervening rings; and so on.

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[1] Otoliths that have been stored dry for a long time float in water; alcohol must then be used.

Since new growth begins about May and continues rapidly throughout the summer and autumn, distinction must be made between fish caught at or near the beginning of the growing season and those caught at or near the end of it. In the early part of the year, before the new seasons's growth has got well under way, a fish whose otoliths record two zones will have completed 2 full years' growth, and really should read '2 zones–2 rings'. By the time the second ring becomes definitely recognizable, the third zone will also be showing up and that fish becomes '3–2'. In late summer and autumn, a fish recording two zones is really aged only 1+; i.e. the second full year's growth is not completed: similarly a three-zoned fish will be 2+, and so on.

Otoliths from a total of 8422 fish, obtained over the years 1936–40 and 1948, have been examined. Of these, readings have been possible from 6261 fish, and 2161 (25·7 %), mainly from individuals over 6 years of age, have been unreadable.

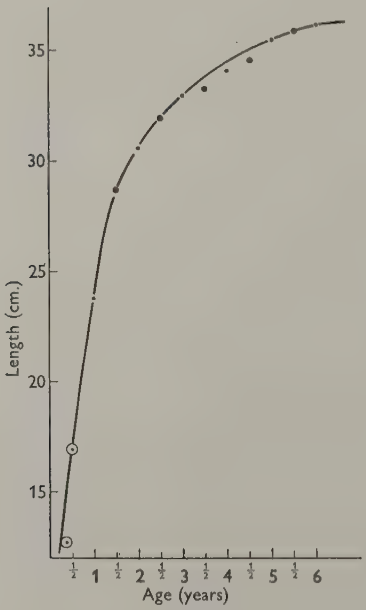
It has been found convenient to group the 6261 fish that gave otolith readings into two groups, 'A' and 'B', the former having 1 September and the latter 1 May as their 'approximate mean date' of capture. Fish included in group A, having the same otolith reading as those of group B, will therefore have a lesser mean length than the latter by the amount of growth that has taken place in the 8 months September to April inclusive.

The mean lengths measured to the nearest centimetre below and suitably corrected, obtained for fishes of different zone readings grouped in this way are given in Table II.

In Text-fig. 1 the lengths of the May fish are plotted against the numbers of otolith zones which, at that time of year, represent fairly exactly the numbers of completed years of growth. A curve has been fitted empirically to those points. The lengths of the September fish can be plotted on the same graph. On inspection it is found that if, in doing so, the number of years' growth recorded in column 2 of Table II as 1+, 2+, ..., be taken to read $1\frac{1}{2}$, $2\frac{1}{2}$, ..., then the points (large on the graph) conform remarkably closely to the curve already drawn for the May fish. This means that September fish with ($n$) zones on their otoliths have completed $(n-\frac{1}{2})$ annual increments of growth; that is to say, that half the total growth increment for the year is completed during the 4 months of May–August inclusive, while the other half is spread over the months September–April inclusive.

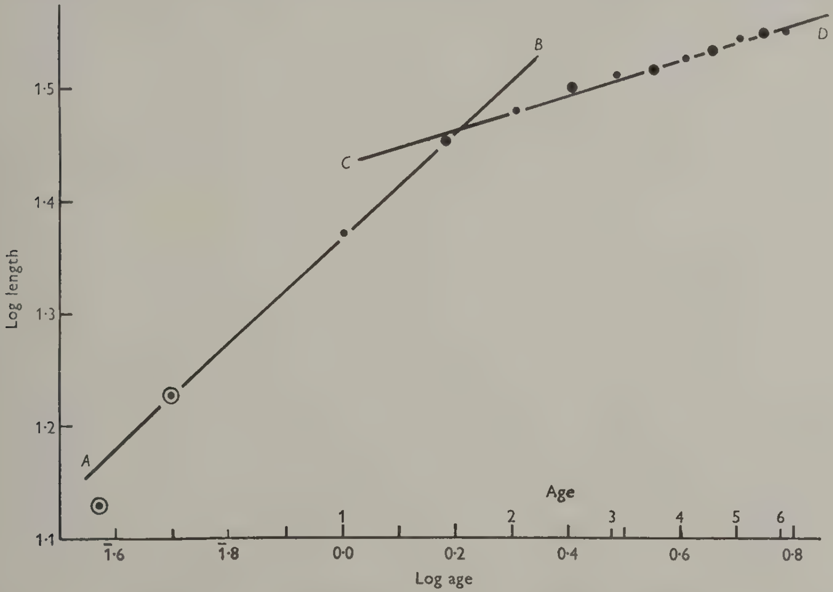
TABLE II. MEAN LENGTHS OF FISH OF DIFFERENT ZONE READINGS (UP TO 6) IN SEPTEMBER AND MAY

| | Mean date, *c.* 1 September | | Mean date, *c.* 1 May | |
|---|---|---|---|---|
| No. of zones on otoliths | No. of years' growth | Mean length | No. of years' growth | Mean length |
| 1 | < 1 | — | No records | |
| | — | — | 1 | 23·8 |
| 2 | 1+ | 28·7 | — | — |
| | — | — | 2 | 30·6 |
| 3 | 2+ | 32·1 | — | — |
| | — | — | 3 | 33·0 |
| 4 | 3+ | 33·3 | — | — |
| | — | — | 4 | 34·1 |
| 5 | 4+ | 34·6 | — | — |
| | — | — | 5 | 35·5 |
| 6 | 5+ | 35·9 | — | — |
| | — | — | 6 | 36·2 |



Text-fig. 1. Growth of mackerel up to 6 years.

Small mackerel of less than 15 cm. in length are seldom caught in this area. Occasionally, however, they put in an appearance in shallow water (Steven, 1948, p. 536). Ford (unpublished data) obtained a few small mackerel in Plymouth Sound in August 1926 having a mean length of 15·3 cm.; and again in August 1927 he caught about fifty similar fish in a sprat seine having a mean length of 13·6 cm. (range 12·5–15·2 cm.). In 1937 very large numbers of small mackerel appeared in and around Newlyn harbour, in Cornwall, and in the first days of August the present writer caught 273 of them having a mean length of 12·7 cm. (range 8·0–16·4 cm.). At the end of the same month 84 more small fish were taken having a mean length of 16·9 cm. (range 14·0–17·9 cm.). Assuming that half a full year's growth takes place, on the average, in May–August inclusive, the fish caught in the first week of August 1937 may be assumed to have made about three-eighths of a full year's growth. The small fish taken at the end of the month would have completed approximately half a year's growth. These points are also plotted (in circles) on the graph in Text-fig. 1 and appear to conform to the curve derived from plotting the age-length relationships of older fish.



Text-fig. 2. Length and age of mackerel—logarithmic plotting.

In Text-fig. 2 the same age-length data are plotted on a double logarithmic scale. When this is done it is found that for fish of 2 years and upwards the points fall on or near the straight line *CD* and that those appertaining to younger fish fall on or near another straight line *AB*, with the exception of the early August fish which do not quite conform. On the assumption that they have grown about three-eighths of their full year's increment, the mean length of these fish should have been 14·6 cm. to fall on the line *AB*, a figure that lies well within the length range of the 273 fish from which the mean was derived and may be accepted as being in reasonable agreement for all practical purposes. On the other hand, an adjustment of 3 weeks in their assumed age is all that is necessary to obtain agreement.

There can be little doubt therefore that in the young fish up to about 2 years of age the growth gradient conformed to that indicated by the line *AB*, which provides the expression

$$L \propto A^{0\cdot49}, \text{ i.e. } A \propto L^{2\cdot06},$$

where $L$ = length in cm., and $A$ = age in years.

In older fish the growth gradient conformed to that indicated by the line *CD*, which provides the expression

$$L \propto A^{0\cdot15}, \text{ i.e. } A \propto L^{6\cdot65}.$$

The two lines *AB* and *CD* intersect at a point representing the logarithms of length 29·3 cm. (limits 28·6–29·5) and age 1·6 years.

It seems likely that this point of discontinuity in the growth gradient represents the approximate length and age at which the onset of active sexual development takes place in the majority of individuals, i.e. that the onset of sexual maturity takes place at a length of about 29 cm. in the second year of life. This means that fish hatched in the spring of any year will begin to 'fill up' in the late autumn of the following year and will spawn for the first time during the subsequent spawning season when approximately 2 full years of age. This is in agreement with Nilsson's statement (1914, p. 41) that 'maturity is reached at the age of 2 years' if by this is meant that the fish arrive at first spawning when they are approximately 2 full years old. Confirmation of these results has been obtained from simultaneous observations on gonad development. Le Gall (1950, p. 71) also states that the onset of first maturity takes place at or over a length of 26–28 cm., but ascribes an age of 3 years to such fish.

## Onset of Sexual Maturity

Data bearing on the onset of sexual maturity in the mackerel of this region have been obtained by examination of 9334 fish in which sex and gonad condition have been determined. The determinations were made by naked-eye observation. Young individuals in which the sex could not be decided by this means have been recorded as immature fish. The later stages of development of the sexual organs have been classified according to a scheme similar to that used internationally for the herring and other clupeoids (see Jensen, 1950, p. 6), but suitably modified for the somewhat special characteristics exhibited by the mackerel.

Stage O. Immature juveniles. Sex not ascertainable by naked-eye examination.

Stage I. Virgin individuals. Sexual organs very small but sex ascertainable by naked eye. Ovaries rich wine colour and very slender torpedo shape; individual eggs indistinguishable. Testes much paler in colour than the ovaries; also thinner and more blade-like.

Stage II. Maturing virgins (maiden fish) and recovering spents. In virgin fish the ovaries are slightly larger now than in stage I and individual eggs begin to be distinguishable. Testes also enlarging; paler in colour than ovaries. In recovering spents, at this stage, both ovaries and testes are also quite small but flabbier than in virgin fish and generally somewhat bloodshot.

Stage III. Sexual organs considerably larger and occupying about half of the ventral cavity. Differences between virgin fish and recovering spents now scarcely distinguishable.

Stage IV. Sexual organs still growing. Ovaries becoming a pronounced orange-yellow colour with conspicuous opaque eggs. Testes becoming a clear creamy or milky colour.

Stage V. Sexual organs now filling ventral cavity. In the ovary superficial blood-vessels have become large and conspicuous. No transparent eggs. Testes assuming a fairly uniform milky whiteness.

Stage VI. *Testes*—large, firm and clean milky white. Small amount of ripe milt can be expelled from them on slight pressure.

*Ovaries.* In the female stage VI has been subdivided into two stages:

Stage (♀) VI A. Ripe translucent eggs scattered throughout unripe eggs giving rise to a 'plum pudding' appearance (see Steven, 1949, p. 565 and plate I). No ripe eggs free in the lumen.

Stage (♀) VI B. Ripe eggs present in the lumen of the ovary which generally must be opened to find them. Externally, the ovary may appear to be in stage V or VI A, but the presence of ripe eggs free in the lumen indicates that one or more batches of eggs have already been spawned. After several batches have been shed the ovary becomes progressively more flabby and bloodshot, especially posteriorly.

Stage VII. *Spent fish.* Ovaries slack with only residual eggs. Very bloodshot. Testes also small, flabby and bloodshot.

A stage VIII as used for herring (Jensen, 1950, p. 6) has not been separately distinguished.

The 9334 fish examined for sex comprised 995 immature juveniles whose sex was not evident from naked-eye observation. The remainder comprised 4031 males and 4308 females. Of these 803 males and 681 females were in maturity stage I—i.e. were virgin fish in which signs of rapid gonad development towards ripening are still absent though the sex is determinable by naked-eye observation. Some females whose lengths ranged from 22 to 28 cm. had ovaries of quite small size that nevertheless exhibited a typically shotten appearance, but which, after the most careful examination, always failed to reveal any residual ripe eggs in the lumen. The explanation appears to be that, in those fish, the gonads had progressed a considerable way towards ripeness and then assumed a spent appearance without any ripe eggs having been actually produced and shed. Similar precocity was detectable also in some males over a length range of 24–28 cm. Since these fish—designated 'false stage VII'—had not spawned, they have been grouped with stages O and I as maiden fish which had not yet reached first maturity.

In Table III the total numbers of fish at the various stages of gonad development have been entered against the length in cm. From this table it will be seen that all fish under 18 cm. in total length were in those stages of immaturity in which the sex was not determinable by naked-eye examination. Fishes in this stage were not uncommon up to a length of 22 cm. after which their numbers diminished and they were almost totally absent in all sizes exceeding 29 cm. Fishes in stage I begin to appear in small numbers at lengths of from 18 to 20 cm. and remain common up to lengths of just over 30 cm. Fishes at stage II, which includes maiden fish with gonads in the very early stages of active ripening, and recovering spents in which the gonads have gone far towards resuming their original appearance in maiden fish, begin to appear at 21 cm. and become plentiful at lengths of 27 cm. and upwards. The later stages, up to and including stage VI, do not appear in any numbers until lengths of 30 cm. and upwards are reached. The table further reveals that spent fish may be at times noticeable in the catches at smaller sizes than fully ripe fish. There are probably two explanations for such apparently anomalous occurrences: (i) that fish in a state of precocious maturity and giving a false appearance of 'spentness' have been mistaken for true spents; and (ii) that, by some vagaries of the fisheries or of sampling, spent fish on occasion were obtained for examination from schools of smallish fish from which no samples were collected when they were in the spawning state.

In further reference to Table III it will be seen that the immature fish of stages O and I and precocious stage VII are chiefly confined to fish of less than 29 cm. in total length—i.e. they are grouped on the left of the line *AB* drawn through the table—and that stages III–VII are comprised mainly of fish of 30 cm. and upwards, i.e. they are grouped on the right of the line *AB*. Stage II may be regarded as a transition phase in which the ripening process is actively beginning but has not yet reached the state of very rapid gonad development associated with stage III onwards.

This grouping of the fish in Table III on either side of a line falling between lengths of 29 cm. and 30 cm. agrees well with the figure of 29·3 cm. as the point of discontinuity in the curve of growth derived from plotting log length against log age. There can be little doubt, therefore, that the change in the growth gradient in respect of the age-length relationship is very closely associated with the onset of first sexual maturity. This is further borne out by the fact that if the percentage of fish exhibiting gonad stages II–VII inclusive (Table III) is plotted against length, the derived sigmoid curve

## TABLE III. LENGTH DISTRIBUTION OF THE VARIOUS REPRODUCTIVE STAGES

Length of fish (in cm.)

A

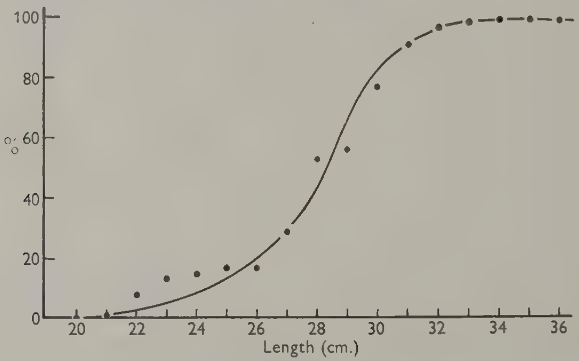
| State of sexual organs | | < 18 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| O: | | 339 | 75 | 88 | 98 | 120 | 122 | 62 | 19 | 19 | 18 | 13 | 9 | 9 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — | 995 |
| I: | ♂♂ | — | 1 | 1 | 3 | 14 | 37 | 52 | 40 | 31 | 67 | 97 | 124 | 179 | 98 | 38 | 15 | 5 | 1 | — | — | — | — | — | — | — | 803 |
| | ♀♀ | — | *1* | *14* | — | *42* | *87* | *63* | *20* | *46* | *92* | *99* | *99* | *72* | *27* | *9* | *7* | *2* | *1* | — | — | — | — | — | — | — | *681* |
| False VII: | ♂♂ | — | — | — | — | — | — | — | 2 | 3 | 14 | 20 | 9 | — | — | — | — | — | — | — | — | — | — | — | — | — | 48 |
| | ♀♀ | — | — | — | — | — | *1* | *2* | *2* | *1* | *2* | *12* | *8* | — | — | — | — | — | — | — | — | — | — | — | — | — | *28* |
| II: | ♂♂ | — | — | — | — | 1 | 1 | 1 | — | 2 | 5 | 9 | 23 | 38 | 51 | 61 | 52 | 34 | 29 | 20 | 10 | 11 | 2 | 2 | 1 | — | 353 |
| | ♀♀ | — | — | — | — | *2* | *21* | *27* | *15* | *17* | *28* | *58* | *145* | *174* | *129* | *64* | *41* | *35* | *35* | *23* | *17* | *7* | *5* | *2* | *1* | — | *846* |
| III: | ♂♂ | — | — | — | — | — | — | — | — | — | — | 1 | — | 1 | 5 | 7 | 31 | 26 | 25 | 13 | 22 | 5 | 4 | — | — | — | 140 |
| | ♀♀ | — | — | — | — | — | — | — | — | — | — | — | *2* | *4* | *10* | *20* | *52* | *89* | *101* | *101* | *60* | *48* | *11* | *5* | *3* | *1* | *507* |
| IV: | ♂♂ | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 5 | 6 | 20 | 29 | 44 | 46 | 39 | 24 | 6 | 13 | — | — | 234 |
| | ♀♀ | — | — | — | — | — | — | — | — | *1* | — | — | — | — | *2* | *11* | *38* | *33* | *59* | *69* | *82* | *64* | *34* | *8* | *1* | *1* | *403* |
| V: | ♂♂ | — | — | — | — | — | — | — | — | 1 | — | — | — | 2 | 6 | 12 | 34 | 78 | 85 | 87 | 83 | 46 | 12 | 4 | 4 | 1 | 455 |
| | ♀♀ | — | — | — | — | — | — | — | — | — | — | — | — | — | *5* | *12* | *43* | *60* | *71* | *82* | *62* | *40* | *25* | *10* | *4* | — | *414* |
| VI: | ♂♂ | — | — | — | — | — | — | — | — | — | — | 2 | 1 | 7 | 61 | 106 | 169 | 231 | 191 | 186 | 149 | 69 | 36 | 13 | — | 1 | 1222 |
| VI A: | ♀♀ | — | — | — | — | — | — | — | — | — | — | — | — | — | *4* | *10* | *19* | *27* | *42* | *29* | *20* | *15* | *7* | *2* | — | — | *175* |
| VI B: | ♀♀ | — | — | — | — | — | — | — | — | — | — | — | — | *2* | *13* | *35* | *72* | *88* | *87* | *70* | *46* | *34* | *23* | *5* | *3* | *2* | *480* |
| VII: | ♂♂ | — | — | — | — | — | — | — | — | 1 | 6 | 17 | 61 | 53 | 64 | 96 | 101 | 131 | 96 | 78 | 46 | 19 | 5 | 1 | 1 | — | 776 |
| | ♀♀ | — | — | — | — | — | — | — | — | *1* | *1* | *10* | *50* | *79* | *80* | *72* | *83* | *95* | *107* | *82* | *68* | *29* | *14* | *2* | *1* | — | *774* |
| Total fish | | 339 | 77 | 103 | 101 | 179 | 269 | 207 | 98 | 123 | 233 | 338 | 531 | 622 | 562 | 560 | 778 | 963 | 974 | 886 | 704 | 411 | 184 | 67 | 19 | 6 | 9334 |
| Total: O, I, False VII | | 339 | 77 | 103 | 101 | 176 | 247 | 179 | 83 | 100 | 193 | 241 | 249 | 260 | 127 | 48 | 23 | 7 | 2 | — | — | — | — | — | — | — | |
| Total II–VII | | — | — | — | — | 3 | 22 | 28 | 15 | 23 | 40 | 97 | 282 | 362 | 435 | 512 | 755 | 956 | 972 | 886 | 704 | 411 | 184 | 67 | 19 | 6 | |
| Percentage II–VII in total fish | | *0·0* | *0·0* | *0·0* | *0·0* | *1·68* | *8·18* | *13·53* | *15·31* | *18·69* | *18·45* | *28·70* | *53·11* | *58·20* | *77·40* | *91·43* | *97·04* | *99·27* | *99·79* | *100·0* | *100·0* | *100·0* | *100·0* | *100·0* | *100·0* | *100·0* | |

B

has its point of inflexion at a length of 28·8 cm. (limits 28·4–29·2) (Text-fig. 3).

## WEIGHT-LENGTH RELATIONSHIP

Weights to the nearest gram of a number of fish covering the whole range of available lengths have been determined. For this purpose fish under 20 cm. in length are arranged in $\frac{1}{2}$ cm. size-groups, measured to the nearest $\frac{1}{2}$ cm. below. Fish over 20 cm. are placed in 1 cm. size-groups, measured to the nearest cm. below. A correction of half a group unit has been added to all mean lengths. The weight-length data so obtained are shown in Table IV. When plotted logarithmically (Text-fig. 4) a definite discontinuity is manifest in the weight-length relationship at 27·9 cm. mean length (with rather wide limits of *c.* 25·7–31·6) and 135 g. mean weight.

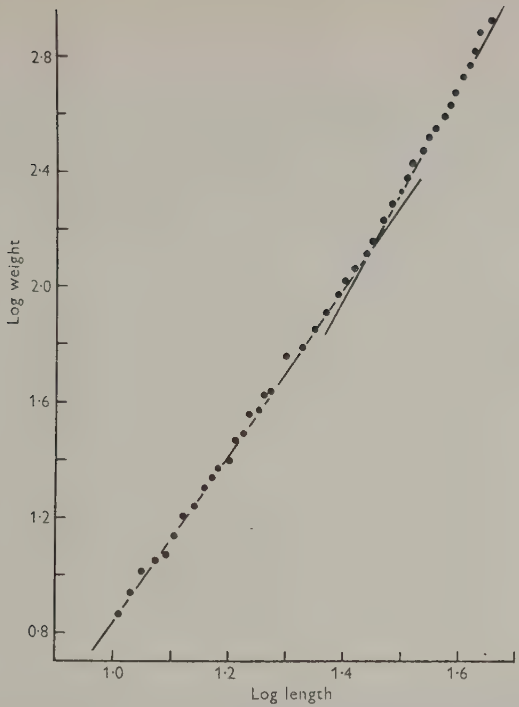


Text-fig. 3. Percentage of all fish examined showing gonad stages II–VII inclusive: in centimetre length-groups.

From 28 cm. down to 10 cm. (the smallest fish weighed) the weight-length relationship is expressed by $W \propto L^{2 \cdot 86}$. From 28 cm. upwards the weight increases much more rapidly in relation to length and conforms to the expression $W \propto L^{3 \cdot 54}$. This applies only to fish in the early part of the year when they have recovered from the spent condition and are again actively ripening; comparative figures for newly spent fish have not been obtained.

A change in the weight-length relationship of growing fish appears to manifest itself at a slightly earlier stage than the change in the length-age relationship, but the difference is doubtfully significant, and anyhow the two critical mean lengths are sufficiently close to suggest that both changes may be initiated simultaneously at the onset of first sexual maturity.

Age determination by direct methods has not been possible beyond 6 years. Further researches and improved techniques may increase the range of direct readings—from otoliths, scales or other body structures—by a few years;



Text-fig. 4. Weight-length relationship of mackerel: logarithmic plotting.

### TABLE IV. WEIGHT-LENGTH RELATIONSHIP

| Length group (cm.) | No. of fish | Mean weight (g.) | Length group (cm.) | No. of fish | Mean weight (g.) | σ |
|---|---|---|---|---|---|---|
| 10·25 | 7 | 7 | 21·5 | 11 | 62 | 4·7 |
| 10·75 | 10 | 9 | 22·5 | 17 | 72 | 6·8 |
| 11·25 | 22 | 10 | 23·5 | 25 | 81 | 7·8 |
| 11·75 | 21 | 11 | 24·5 | 33 | 95 | 8·0 |
| 12·25 | 32 | 12 | 25·5 | 26 | 105 | 12·9 |
| 12·75 | 32 | 14 | 26·5 | 18 | 115 | 8·6 |
| 13·25 | 38 | 16 | 27·5 | 26 | 129 | 9·3 |
| 13·75 | 25 | 17 | 28·5 | 39 | 146 | 17·0 |
| 14·25 | 26 | 20 | 29·5 | 49 | 169 | 12·0 |
| 14·75 | 32 | 22 | 30·5 | 49 | 194 | 14·3 |
| 15·25 | 20 | 24 | 31·5 | 54 | 217 | 16·2 |
| 15·75 | 10 | 25 | 32·5 | 60 | 241 | 17·7 |
| 16·25 | 14 | 30 | 33·5 | 72 | 271 | 23·6 |
| 16·75 | 12 | 31 | 34·5 | 96 | 300 | 25·0 |
| 17·25 | 2 | 37 | 35·5 | 77 | 331 | 31·7 |
| 17·75 | 5 | 37 | 36·5 | 100 | 354 | 35·9 |
| 18·25 | 1 | 42 | 37·5 | 88 | 392 | 44·5 |
| 18·75 | 3 | 43 | 38·5 | 67 | 430 | 47·0 |
| 19·25 | — | — | 39·5 | 43 | 481 | 34·4 |
| 19·75 | — | — | 40·5 | 24 | 542 | 55·8 |
| 20·5 | 6 | 58 | 41·5 | 8 | 584 | 29·1 |
|  |  |  | 42·5 | 6 | 669 | 24·3 |
|  |  |  | 43·4* | 3 | 782 | — |
|  |  |  | 46·1† | 1 | 851 | — |

Specimens up to 20 cm. in length were weighed all together in their length groups and the mean obtained by a single calculation: σ was therefore not obtained.

* Actual mean (without correction) of fish measured to nearest mm.

† Actual measurement to nearest mm.

but such determinations are unlikely in the foreseeable future to cover the entire life span. It is worth while, therefore, to use the data already available to calculate approximate theoretical mean lengths and mean weights attained by fish in each year of life until a length of 43 cm. is reached—this being the maximum length recorded in this investigation, except for a single fish of 46·1 cm. total length weighing 851 g.

TABLE V. LENGTH AND WEIGHT OF MACKEREL AT DIFFERENT AGES UP TO 20 YEARS: UP TO 6 YEARS FROM DIRECT OBSERVATION, THENCE BY CALCULATION

| Age (years) ... | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| Approximate mean length (cm.) | 23·8 | 30·6 | 33·0 | 34·1 | 35·5 | 36·2 | 37·1 | 37·8 | 38·5 | 39·1 |
| Approximate mean weight (g.) | 80 | 188 | 247 | 278 | 322 | 345 | 381 | 410 | 436 | 462 |
| Age (years) ... | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| Approximate mean length (cm.) | 39·7 | 40·2 | 40·7 | 41·1 | 41·5 | 41·9 | 42·3 | 42·7 | 43·0 | 43·4 |
| Approximate mean weight (g.) | 486 | 509 | 532 | 553 | 574 | 594 | 614 | 633 | 651 | 669 |

According to these calculations the single 46·1 cm. fish obtained during these investigations would be 30 years old and should weigh approximately 832 g.

## ACKNOWLEDGEMENTS

The investigations described here and in Parts I and II benefited very greatly from abundant help and advice freely given by many persons. Chief amongst them was Skipper B. Moore of the Lowestoft steam drifter 'B.T.B.' (L.T. 1153), who took a keen interest in the work from its inception and on two occasions put his ship at my disposal for special cruises. Other drifter skippers who helped in various ways were E. W. J. Capps (L.T. 89, *Present Friends*), J. R. Capps (L.T. 240, *Justified*), W. A. Capps (L.T. 145, *Silver Prince*), F. Darkins (L.T. 244, *Justifier*), H. Darkins (L.T. 730, *Implacable*), R. Green (Y.H. 497, *Young John*), A. W. Jackson (L.T. 172, *True Reward*), W. G. Jenner (L.T. 89, *Present Friends*), W. C. Julings (L.T. 277, *Oak Apple*), T. Lane (Y.H. 105, *Wydale*), H. Muttett (L.T. 730, *Implacable*), S. Spilling (Y.H. 711, *Harry and Leonard*), W. Thompson, senr. (L.T. 756, *Buckler*), W. Thompson, jun. (L.T. 1217, *Golden Chance*), L. Tooke (L.T. 256, *Welcome Home*), A. R. J. Warner (Y.H. 471, *Ocean Swell*), A. W. Wilkinson (Y.H. 141, *Playmates*), E. J. H. Tallop (L.T. 711, *Lord Fisher*) and Skipper W. H. E. Nicholls of the steam trawler *Elk* (M. 36).

On the fish-market at Newlyn, Cornwall, where most of the field work was done, Mr T. Cotton, Clerk to the Harbour Commissioners and the late Captain D. Oliver, Harbourmaster, gave invaluable assistance. It is a pleasure to record my indebtedness also to all the fish-merchants and their employees at Newlyn and to the manager and staff of the Newlyn branch of the Great Grimsby Coal, Salt and Tanning Co. Ltd., for much help and advice. To the

Newlyn Harbour Commissioners, both individually and collectively, I am grateful for numerous facilities willingly granted. My best thanks are also due to Mr G. M. Spooner for statistical guidance and to Dr H. G. Vevers for translations from Norwegian publications. Mr P. G. Corbin helped with some of the field work, and Mr A. D. Mattacola provided the photographs for Pl. I.

## SUMMARY

Owing to the difficulty of age-determination in mackerel, the age and growth rate of these fish had not previously been satisfactorily determined.

Two schools of thought arose, one attributing a length of little over 10 cm. at the end of the first year of life, while the other ascribed lengths of up to about 25 cm. to 1-year-old fish.

The present investigation supports the second school. Direct age-readings from scales and otoliths have been made of fish up to 6 years of age, and the probable sizes at greater ages have been calculated.

There appears to be a critical change in growth characteristics at a mean length of about 29 cm., coinciding with the first ripening of the genital products.

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## EXPLANATION OF PLATE I

Fig. 1. Mackerel scale showing one ring and two zones: × 55. From a fish 28 cm. in length, 9 October 1936.

Fig. 2. Mackerel scale showing two rings and three zones: × 44·3. From a fish 33 cm. in length, 8 June 1937.

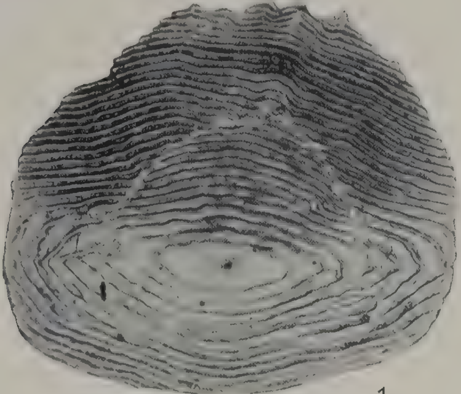
Fig. 3. Mackerel scale showing three rings and four zones: × 48·5. From a fish 34 cm. in length, 24 September 1936.

Fig. 4. Otolith showing one ring and two zones: × 12·8. From a fish 29 cm. in length, 22 September 1936.

Fig. 5. Otolith showing two rings and three zones: × 12·4. From a fish 33 cm. in length, 23 July 1936.

Fig. 6. Otolith showing three rings and four zones: × 12·05. From a fish 34 cm. in length, 22 September 1936.

The illustrations in this plate are all from un-retouched photographs.



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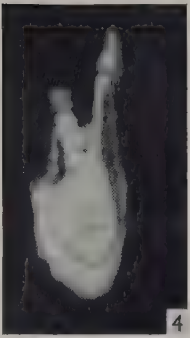

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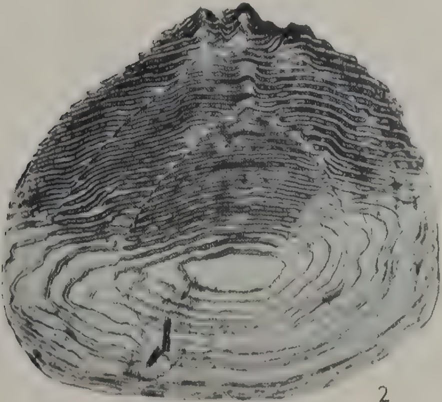

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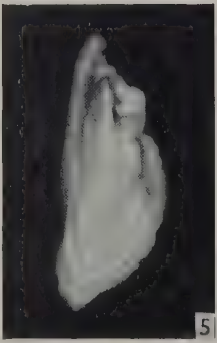

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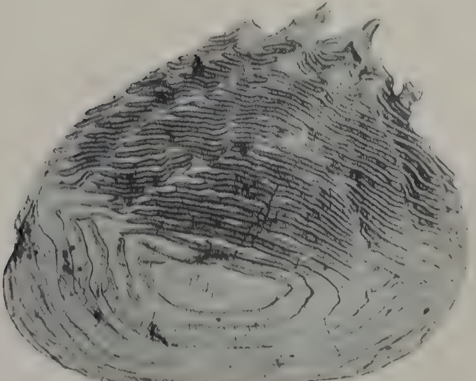

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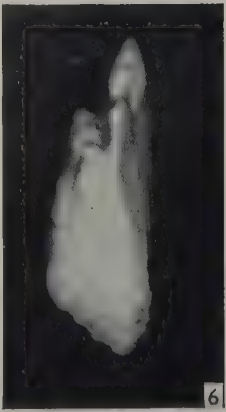

6

# THE BIOLOGY OF *ASTERIAS RUBENS* L. III. CAROTENOID PIGMENTS IN THE INTEGUMENT

By H. G. Vevers, M.A., D.Phil.

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In the Plymouth area there is often a marked and consistent difference in coloration of starfishes (*Asterias rubens*) from different populations. Starfish from populations to the south of Plymouth Breakwater are red-brown or occasionally pale yellow-brown in colour, whereas those from a population living well within Plymouth Sound have been found to be consistently bright red or brick red in colour (Vevers, 1949). In the present work analysis has been made of the integumentary carotenoids of dark red-brown *A. rubens* taken from the trawling grounds between Plymouth Breakwater and the Eddystone.

The asteroids are usually richly coloured, and investigation of a number of species has shown the almost universal occurrence of carotenoid pigments in the integument. In addition to the carotenoids, MacMunn (1886), working at the Plymouth Laboratory, extracted a porphyrin pigment which he identified as haematoporphyrin from the integument of *A. rubens*. It is now known that haematoporphyrin does not occur in nature, and a re-examination of the porphyrin pigments of this species is in course of preparation (Kennedy & Vevers).

Cuénot (1887) observed that the integument of starfishes consists of three distinct layers: the internal epithelium, which lines the general body cavity and which is not concerned with the external pigmentation of the animal, a median conjunctive layer, in the outer part of which the calcareous plates are deposited, and an external epithelium of tall, elongated cells, covered by a cuticle, through which the cilia protrude. The external epithelial cells with the cuticle make up the epidermis. The majority of the epidermal cells are narrow and columnar, with their inner ends resting on a basement membrane which divides the epidermis from the median conjunctive layer (Ludwig & Hamann, 1899). Scattered among these more generalized epidermal cells are two types of more specialized cells, the mucus gland cells, which are particularly frequent in *A. rubens*, and the mulberry cells, first described by Cuénot (1887) and of unknown function.

Ludwig & Hamann (1899) stated that, in general, the integumentary pigments of starfishes are deposited in the epidermal layer. Cuénot (1887) found that in *Echinaster sepositus* a red pigment was deposited in the epidermis, and in the present work it was found that most of the carotenoid pigment of the integument is contained in the unspecialized columnar epithelial cells. There are no special chromatophores.

## CAROTENOID PIGMENTS IN THE INTEGUMENT

Abeloos (1926) observed that the carotenoids in the integument of *Asterias rubens* were sometimes present in the form of complexes produced by the conjugation of a carotenoid with a protein radical. Lönnberg (1931, 1933, 1934) extracted carotenoids from a large number of marine invertebrates, including *A. rubens*. In most he was able to partition the crude extracts into an epiphase (in petroleum ether) and a hypophase (in 90 % methanol). He did not, however, use any chromatographic adsorption technique for the separation of the pigments, and in general his results only indicated that at least one and probably two carotenoid pigments were present in the integument of *A. rubens*.

Von Euler & Hellström (1934) isolated a carotenoid acid from the aboral integument of *A. rubens*, which they named 'Asterinsäure'. Karrer and Rübel (Karrer & Jucker, 1948, p. 351) subsequently obtained a yield of astacene from this species, and Karrer & Jucker (1948, p. 351) now consider that 'Asterinsäure' is probably identical with astacene (or astaxanthin).

### *Experimental*

In the present work on the separation of the integumentary carotenoids only dark red-brown specimens of *A. rubens* were used. For analysis by Methods 1 and 2, aboral integument was finely chopped and ground up with dry acid-washed silver sand (the sand was washed with HCl, and then with three changes of water before being dried). The integument was then extracted with successive portions of acetone, until no further colour appeared in the extract. Petroleum ether (b.p. 40–60° C.) was added to the acetone extract, and the volume of the whole extract was doubled by addition of distilled water. After gentle shaking, the pigment passed from the acetone-water fraction to the petroleum ether, which was dried by shaking with anhydrous sodium sulphate. The petroleum-ether extract of the total carotenoids was then divided into two parts for further analysis by either Method 1 or Method 2.

*Method* 1. The petroleum-ether extract was chromatographed on bone meal (B.D.H. bone meal for carotene estimations). Continued elution with petroleum ether removed Fraction 1*a*, which was then passed through a column of alumina (B.D.H. aluminium oxide for chromatographic adsorption analysis) on which it formed two bands. The lower band was removed by elution with more petroleum ether and collected separately as Fraction 1*b*, and the upper band, which was the richest in colour, was eluted by petroleum ether containing 5 % (v/v) of acetone to give Fraction 1*c*. The pigment remaining on the bone meal column was eluted by acetone and collected as a pale straw-yellow solution (Fraction 1*d*).

Fraction 1*b* was divided into two parts and each was separately evaporated almost to dryness over a water-bath, the final traces of liquid being removed in a stream of carbon dioxide. The residues were dissolved in carbon disulphide and petroleum ether respectively. Absorption spectra (Table I) of each of these solutions were recorded with a 'Unicam S.P. 500 Quartz Spectrophotometer'. The absorption maximum obtained for the solution in carbon disulphide is identical with that recorded by Karrer & Jucker (1948) for $\beta$-carotene. The absorption maximum for the solution in petroleum ether is very close to that obtained for $\beta$-carotene by Morton & Rosen (1949).

In order to confirm that Fraction 1 *b* was $\beta$-carotene a mixed chromatogram was used. The petroleum-ether solution of the pigment was mixed with a solution of known $\beta$-carotene in the same solvent and the mixture chromatographed on a long column (15 × 1 cm.) of alumina. A single band was formed which did not split on slow elution with petroleum ether.

TABLE I. ABSORPTION MAXIMA OF CAROTENOID FRACTIONS IN M$\mu$

| Fraction | Carbon disulphide | Pyridine | Petroleum ether |
|---|---|---|---|
| 1 *b* | 485 | — | 449 |
| 1 *c* | 503 | 489 | — |
| 2 *b* | 485 | — | 449 |
| 2 *c* | 509 | 497–502 | — |

Fraction 1 *c*, which was also epiphasic, was divided into two parts, each of which was evaporated to dryness and the residues dissolved in carbon disulphide and pyridine respectively. This fraction gave strong, well-coloured solutions, and spectrophotometer readings gave the absorption maxima recorded in Table I.

These maxima agree very closely with those given by Goodwin & Srisukh (1949) for esterified astaxanthin. This agreement, together with the fact that Fraction 1 *c* was always epiphasic when shaken with a mixture of petroleum ether and 90 % methanol, leaves no doubt that the pigment in this fraction was esterified astaxanthin. It should be noted that the esterified astaxanthin (Fraction 1 *c*) originally formed part of Fraction 1 *a*, which was eluted from the bone-meal column with petroleum ether. This elution is similar to the experience of Morton & Rosen (1949), who found that esterified 'xanthophyll' was sometimes carried through a bone-meal column with light petroleum.

Fraction 1 *d* was collected from the bone-meal column by elution with acetone. It was taken into petroleum ether and partitioned between this solvent and 90 % methanol. The pigment was found to be entirely hypophasic, suggesting the free forms of xanthophylls. From this solution it was taken back into petroleum ether, evaporated to dryness and dissolved in benzene. The benzene solution was chromatographed on zinc carbonate, and a single band formed which was eluted with ether containing 3 % methanol (v/v). The yield from this fraction was never sufficient to give a good sample for spectrophotometric measurement, but its behaviour on phase partition and chromatography suggested that it contained one pigment only of the free xanthophyll type, possibly lutein or zeaxanthin.

*Method* 2. The remainder of the total carotenoid extract was partitioned between petroleum ether and 90 % methanol to give an epiphasic fraction (2*a*) and a hypophasic fraction (2*d*) respectively. Fraction 2*a* contained nearly all the pigment. It was evaporated to dryness slowly on a water-bath, the final traces of solvent being removed in a stream of $CO_2$. To the residue were added 2 ml. ethanol and 1 ml. of KOH (concentration of 160 g. KOH in 106 ml. $H_2O$), and this saponification mixture was heated and kept just bubbling for 3 min. The residue was cooled by adding distilled water and then extracted with ethyl ether. Some of the pigment passed into the ether but most remained in the lower layer of aqueous ethanolic KOH. On addition of a few drops of glacial acetic acid, followed by gentle shaking, all the pigment passed into the ether. (It is characteristic of astacene that it remains hypophasic in alkaline solution, even in the presence of excess water.) The ether extract was then evaporated to dryness and dissolved in petroleum ether. On addition of an equal volume of 90 % methanol partition took place to give an epiphase (Fraction 2*b*) and a hypophase (Fraction 2*c*).

Fraction 2*b* was dried over anhydrous sodium sulphate, and chromatographed on a column of alumina. Slow elution with the solvent failed to split the single band of pigment which was finally collected in a flask. This fraction was then examined in the spectrophotometer in $CS_2$ and in petroleum ether, and the maxima recorded were the same as those for $\beta$-carotene in Fraction 1*b* above.

Fraction 2*c* was taken from 90 % methanol into petroleum ether, and divided into two parts each of which was evaporated to dryness over a water-bath. The residues were dissolved in $CS_2$ and pyridine respectively and recordings made of the absorption spectra (Table I).

The positions of these maxima (cf. Karrer & Jucker, 1948, p. 242) and the behaviour of this fraction after saponification suggest that the pigment was astacene. Kuhn & Sörensen (1938) have shown that astacene does not occur naturally, but is produced in the course of saponification by the oxidation of astaxanthin. As the fraction from which the present yield of astacene was derived was originally epiphasic, it is probable that it was present in the integument in the form of esterified astaxanthin. This would agree with the finding of esterified astaxanthin in Fraction 1*c*.

Fraction 2*d* was very faint in colour. It was treated in the same way as Fraction 1*d*, and behaved the same way on chromatography. It probably represents the small amount of free xanthophyll found in Fraction 1*d*.

As a further check on the identity of the carotenoid pigments, and in order to test for the existence of a carotenoid-protein complex, a third system of extraction was used (Method 3).

*Method* 3. The integument was ground up with silver sand and extracted in the first place with *n*-hexane to remove all the carotenoids which were not bound to a protein. This gave Fraction 3*a*. The residue of tissue was then extracted with acetone to give Fraction 3*b*.

Fraction 3*a* was relatively pale in colour. By means of phase partition and chromatography it gave weak solutions of β-carotene, esterified astaxanthin, and a free xanthophyll.

Fraction 3*b* was strong in colour and contained the greater part of the integumentary carotenoid pigment. It was entirely epiphasic and was found to contain esterified astaxanthin only. There was no evidence that β-carotene occurred in this fraction.

I am indebted to Dr W. R. G. Atkins, F.R.S., and Dr C. F. A. Pantin, F.R.S., for reading and criticizing the manuscript.

## DISCUSSION

It is probable that the carotenoid pigments extracted from *A. rubens* by Lönnberg were not always fully separated into their constituents prior to spectroscopic determination. The presence of astaxanthin in this species was first noted by Karrer and Rübel. This has been confirmed in the present work, and it has also been found that in the integument it is present in the esterified form. The astaxanthin found in *A. rubens* is very closely comparable with that extracted from the hypodermis of *Homarus vulgaris* and *Nephrops norvegicus* by Goodwin & Srisukh (1949), and there is no doubt that, from the point of view of colour production, it is the most important of the integumentary carotenoids in *A. rubens*. In the dark-brown specimens of *A. rubens* used in the present investigation the greater part of the esterified astaxanthin is linked with a protein. This is similar to the condition found in the carapace and eggs of *Astacus gammarus* by Kuhn & Sörensen (1938). Carotenoids have also been extracted from a number of Pacific Coast echinoderms, including four species of asteroids, by Fox & Scheer (1941), but the yields were usually from the whole body, and so are not strictly comparable with the present results. They did, however, find that one of the predominant carotenoids in the asteroids was astaxanthin, but they did not record any protein linkage.

## SUMMARY

A preliminary analysis of the integument of dark-brown specimens of *Asterias rubens* has shown that the carotenoid pigments present are astaxanthin, β-carotene and a free xanthophyll. The last two occur only in small amounts. The astaxanthin is present in the esterified form, and represents the greater part of the total carotenoids.

Most of the astaxanthin is present in the form of an astaxanthin-protein complex, which is coloured brown or dark brown in the living animal.

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# TRACE ELEMENTS IN THE COMMON BROWN ALGAE AND IN SEA WATER

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## INTRODUCTION

Sea water probably contains all the chemical elements, although a number of them have not yet been detected. Considerable information is available on the occurrence of various elements in marine plants and animals, but it is far from complete for any one biological group. Except for recent work by Spooner (1949), on the absorption of radioactive strontium and yttrium by marine algae, no detailed study of the trace elements in the brown algae, nor any attempt to correlate the trace elements in sea water with those in the algae, appears to have been carried out. The following is a brief résumé of the work that has been done in this field.

The distribution and concentration of iodine in the sea have received a great deal of attention because of their important roles in the physiology of man and terrestrial animals. The form in which iodine occurs in sea water is not clearly understood, but part of it is present as iodide and iodate. It is concentrated to a marked degree by the marine algae, and for many years the Phaeophyceae were used as a commercial source of iodine. The concentration of iodine and its seasonal variation in the brown marine algae have already been reported (Black, 1948*a*, *b*, 1949).

Considerable interest has recently been shown in the content of radioactive elements in sea water. Studies by Evans, Kip & Moberg (1938), and by Föyn, Karlik, Pettersson & Rona (1939), have shown that the radium content measured by the radon emanation technique varies between about 0·2 and $3{\cdot}0 \times 10^{-7}\,\mu$g./l. in sea water of salinity approximately 35‰. These workers found that organisms concentrate the radium about one-hundredfold in their soft tissues, and calcareous structures show an increase in the radium : calcium ratio over that in the water. In a search for the radioactive precursors of radium, Karlik analysed a number of samples from various parts of the oceans and obtained a mean value of $1{\cdot}5\,\mu$g./l. for uranium (Föyn *et al.* 1939).

Tables giving the trace elements which have so far been determined in sea water have been compiled by Sverdrup, Johnson & Fleming (1942, pp. 176–7), Harvey (1945, pp. 31–2), and Legendre (1947).

In 1919, Cornec carried out the first spectrographic analysis of marine plants and found the following elements: Ag, As, Co, Cu, Mn, Ni, Zn, Bi, Sn, Ca, Mo, Au, Sb, Ti, W and U. The analysis, however, was qualitative and the species investigated were not given.

The distribution of arsenic in marine algae has been studied by Jones (1922), and by Williams & Whetstone (1940). Jones determined the arsenic content of eleven varieties of British seaweeds and obtained a value of 125 mg./kg. for *Laminaria digitata*.

The titanium in a number of cryptogamic plants has been estimated by Bertrand & Voronca-Spirt (1930), while Meulen (1932) determined molybdenum in several species of algae and reported a figure of 0·16 mg. Mo/kg. dry weight.

Webb (1937), in his studies on the ultimate composition of biological material, carried out a spectrographic analysis of marine invertebrates and included the three algae, *Ulva lactuca* (frond), *Fucus serratus* (receptacles) and *Saccorhiza bulbosa* (stipes). Figures are given for Na, K, Ca, Mg, Sr, Ba, B, Al, Mn, Fe, Cu and Pb.

In 1938, Igelsrud, Thompson & Zwicker found the boron content of five marine algae to be 4·2–14·9 mg. B/kg. dry material, and Lagrange & Tchakirian (1939) examined *Lithothamnium* and detected spectrographically in the ash, apart from ordinary constituents, Ag, As, Be, Cu, Ge, Mn, Mo, Ni, Pb, Sb, Sn, Ti, U, W and Zn. The rare earths in similar algae have been examined by Servigne & Tchakirian (1939), who analysed the ashes of *L. calcareum* and found about 5 mg./kg. of Pr, Nd and Sm.

The radium content of a number of algae has been determined by Wiesner (1938). Seven fresh-water and sixteen salt-water algae from different localities were examined, and the results indicated considerable accumulation of radium by the plants.

In 1940, Öy discussed the physiological importance of iron, copper, manganese and boron, and determined these elements in several species of algae. Iron varied between 120 and 1330 mg./kg. dry matter, while *Ascophyllum nodosum* contained 1·1–1·4 mg./kg. copper, *Laminaria* 4 mg./kg., *Fucus serratus* 5·8–17·4 and *F. vesiculosus* 3·4–8·4 mg./kg. Manganese was present in the Fucaceae to the extent of 100–130 mg./kg., and boron 100 mg./kg.

A spectrographic analysis of a dried seaweed meal carried out by the Macaulay Institute for Soil Research was reported by Beharrell in 1942; and in 1941 Wilson & Fieldes estimated spectrographically eighteen of the minor elements of *Macrocystis pyrifera*. No further work appears to have been carried out since that time.

## EXPERIMENTAL

With the exception of *Laminaria cloustoni*, which was collected at Cullipool, Luing Island, Argyllshire, and one sample of *L. digitata* from Ardencaple

Bay, Seil Island, Argyllshire, all the samples of algae were collected at Atlantic Bridge, which joins the Island of Seil with the mainland of Scotland.

Immediately after collection the samples were air-dried at 25–30° C. for 48 hr., with every precaution taken to prevent metallic contamination and, with the exception of the last two sets of samples, were milled in a small porcelain-edge runner mill. With the later samples, however, the milling was carried out in a Christy and Norris no. 8 laboratory mill.

The sea-water samples were collected 20 miles off Plymouth[1] at 20 m., and from ½ m. at Atlantic Bridge and Ardencaple Bay. In the first series of experiments the samples of sea water were stored both in Pyrex and Polythene bottles, but the analyses were identical, thereby indicating that no difference in composition has resulted from diatoms adhering to the glass surface or from the straight surface adsorption of trace elements on the glass. Pyrex bottles were therefore used for the remainder of the samples.

In Table I, the washed frond of *L. digitata* was obtained by soaking the whole frond in 5 gallons of ordinary tap water for 24 hr., prior to air-drying and milling.

## ANALYTICAL METHODS USED

The trace-element analyses reported in this paper were carried out at the Macaulay Institute for Soil Research by a cathode layer arc spectrochemical technique, differing only in detail from that employed for plant materials (Mitchell, 1948). For a few elements semi-quantitative assessments only were made, but unless specifically indicated the results were obtained by a quantitative technique: directly on the ashed material (Farmer, 1950) for Cu, Ba, Sr, Mn, and by a method involving chemical concentration prior to spectrographic analysis (Mitchell & Scott, 1948) for Co, Ni, Mo, Fe, Pb, Sn, Zn, V, Ti, Cr and Ag. Even after concentration of the 100-fold order one or two of the elements reported, notably Sn, Ag, and in a few instances Pb, are close to the lower limit of determination, and these results may be somewhat less reliable than those for the other elements.

## DISCUSSION OF RESULTS

As with the major constituents of seaweed the results indicate that the content of trace elements depends on the species and on the stage of development, and that there is probably appreciable seasonal variation.

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[1] The following determinations have been made on the 20 m. sample collected off Plymouth:

| | Determination | Observer or analyst |
|---|---|---|
| Temperature | 9·28° C. | Mr F. A. J. Armstrong |
| Salinity | 35·12 ‰ | Government chemist |
| Inorganic phosphate | 16·0 μg./l. P | Mr F. A. J. Armstrong |
| Total phosphorus | 19·2 μg./l. P | Mr F. A. J. Armstrong |

No doubt some variation will occur in different habitats, where natural deposits and land drainage may influence the trace elements in the inshore waters where the algae are growing, but this has not been investigated.

It has already been shown (Black, 1948*a*, *b*, 1949) that iodine varies considerably in the different species and even in the same species, showing a progressive increase with the depth of immersion of the plant, increasing, for example, from 0·03% (dry basis) in *Pelvetia canaliculata* and *Fucus spiralis* to over 1% in *Laminaria cloustoni*. Although the seasonal variation is somewhat erratic, the iodine, which exists both in the organic and inorganic form, is generally at a maximum when the total ash and crude proteins are at a maximum. With the trace elements the reverse is true. In general, the trace elements are higher in May than in January and there appears to be no correlation between the trace-element content and the total mineral matter. If the phenomenon of trace-element concentration is one of ion exchange (Wassermann, 1949), it is reasonable to find that the concentration varies with the stage of development of the plant. The stipe which is perennial is consequently higher in these elements than the frond. It may also be, however, that the trace elements in the frond are utilized in sporogenesis, etc. It is interesting to find, therefore, that many of the trace elements such as Co, Ni, Mo, Fe, etc. (Table II), which may be essential for reproduction, are lower in a sporing than in a sterile frond.

TABLE I. TRACE-ELEMENT CONTENTS OF *LAMINARIA* FRONDS IN MG./KG. OVEN-DRIED MATERIAL

| | *Laminaria digitata* frond. Collected July 1948, unwashed | *Laminaria digitata* frond. Collected July 1948, washed | *Laminaria cloustoni* frond. Collected Oct. 1947, unwashed |
|---|---|---|---|
| Total ash (% of dry matter) .... | 24·2 | 11·8 | 13·8 |
| Estimations quantitative | | | |
| Co | 0·21 | 0·31 | 0·21 |
| Ni | 1·7 | 1·40 | 0·9 |
| Mo | 0·16 | 0·21 | 0·16 |
| Pb | — | 20 | 13 |
| Sn | 3·8 | 1·0 | 1·0 |
| Zn | 148 | 93 | 59 |
| V | 0·4 | 1·9 | 1·1 |
| Ti | 3 | 52 | 21 |
| Cr | 1·5 | 1·8 | 0·9 |
| Ag | 0·2 | 0·2 | 0·2 |
| Fe | 292 | 402 | 314 |
| Estimations semi-quantitative | | | |
| Cu | 120 | 70 | 30 |
| Rb | 25 | 80 | 30 |
| Li | 1 | 4 | 2 |
| Ba | 80 | 100 | 30 |
| Sr | 400 | 800 | 400 |
| Mn | 12 | 30 | 15 |

Soaking a fresh *Laminaria* frond in water, although it removes a considerable amount of the water soluble mineral matter presumably in solution in the cell sap, does not remove the trace elements, which appear, therefore, to be in an insoluble form, possibly adsorbed on the colloids present, or combined with the polysaccharides such as alginic acid or fucoidin (Table I).

Samples of the various species collected in January 1949 (Table II) show considerable variation in trace-element contents, and *Fucus serratus* appears to be exceptional in concentrating iron to 717 mg./kg. and manganese to 800 mg./kg.

A comparison of the trace elements in a sporing and non-sporing frond of *Laminaria cloustoni* shows slight differences, and it may be, therefore, that the trace elements are utilized to some extent in reproduction.

A further set of samples taken in May 1949 shows that on the anhydrous basis the trace elements undergo quite appreciable seasonal variation. Despite the fact that the total ash has decreased the trace-element content shows considerable increases (Table III), e.g. in *Pelvetia canaliculata* nickel increases from 1·9, iron from 195, and titanium from 11·4 mg./kg. in January 1949, to 3·7, 565 and 37·8 mg./kg. respectively in May.

The samples taken in June 1950 (Table IV) differ quite appreciably from those taken in May 1949 (Table III). With the exception of *Fucus serratus*, the iron content, for example, is considerably higher in the 1950 samples, but this might be due to metal contamination, as the 1950 samples were milled in a C. and N. Mill, while the others were ground in a porcelain-edge runner mill.

The results in Table IV again show the differences which occur in the trace-element content of different species from the same habitat, with *F. spiralis* unaccountably high in most of the trace elements, for example, 308 mg./kg. of titanium as compared with 4 mg./kg. in *Laminaria digitata* frond. At this time of the year the dry-weight content of *Fucus spiralis* is very low, the plant having taken in large volumes of water preparatory to shedding its gametes. This is further evidence of a correlation which may exist between the trace-element content and the reproductive cycle of the plant. Even when the results are calculated on the wet basis (Table V) *F. spiralis* still contains higher concentrations of the trace elements, particularly titanium and iron, than the Laminariaceae.

Despite the fact that one of the samples of sea water was taken in February, 20 miles off Plymouth at a depth of 20 m., and the other from inshore waters at Ardencaple Bay and Atlantic Bridge in June, the differences in the trace elements estimated are quite insignificant, but the contents are higher than those recorded in the literature (Table VI).

In Table VII the 'concentration factor' shows the extent to which marine algae can concentrate the trace elements, *F. spiralis* containing 10,000 times more titanium than the surrounding sea water, although the majority of the factors are smaller.

TABLE II. TRACE-ELEMENT CONTENTS OF OVEN-DRIED SEAWEEDS (COLLECTED 12 JANUARY 1949) IN MG./KG.

| Sample | Total ash (% of dry matter) | Co | Ni | Mo | Fe | Pb | Sn | Zn | V | Ti | Cr | Ag | Rb | Li | Sr | Ba | Mn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pelvetia canaliculata* | 24·6 | 0·37 | 1·9 | 0·34 | 195 | 4 | 0·8 | 40 | 1·2 | 11 | 0·6 | 0·2 | 100 | 6 | >2400 | 70 | 70 | 5 |
| *Ascophyllum nodosum* | 27·2 | 0·41 | 1·5 | 0·69 | 168 | 6 | 1·0 | 103 | 1·9 | 9 | 0·7 | 0·3 | 80 | 4 | 2600 | 50 | 50 | 4 |
| *Fucus serratus* | 27·4 | 0·47 | 1·6 | 0·40 | 717 | 21 | 1·2 | 79 | 3·3 | 9 | 2·6 | 0·6 | 170 | 6 | >2800 | 80 | 800 | 11 |
| *Laminaria digitata* frond | 41·5 | 1·46 | 8·2 | 0·32 | 350 | 13 | 0·7 | 99 | 2·0 | 20 | 1·1 | 0·4 | 240 | 8 | 4000 | 120 | 80 | 20 |
| *L. digitata* stipe | 39·7 | 0·43 | 3·2 | 0·15 | N.d. | N.d. | N.d. | N.d. | 2·2 | 16 | 1·4 | 0·2 | 240 | 4 | 4000 | 60 | 100 | 16 |
| *L. cloustoni* frond, sterile | 32·4 | 0·56 | 2·0 | 0·50 | 283 | 10 | 0·7 | 117 | 1·3 | 19 | 1·2 | 0·7 | 250 | 6 | 3000 | 60 | 30 | — |
| *L. cloustoni* frond, sporing | 22·4 | 0·35 | 1·5 | 0·24 | 226 | 26 | 1·0 | 136 | 1·0 | 20 | 1·2 | 0·5 | 130 | 4 | 2200 | 65 | 30 | 15 |

TABLE III. TRACE-ELEMENT CONTENTS OF OVEN-DRIED SEAWEEDS (COLLECTED 26 MAY 1949) IN MG./KG.

| Sample | Total ash (% of dry matter) | Co | Ni | Mo | Fe | Pb | Sn | Zn | V | Ti | Cr | Ag | Sr | Ba | Mn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pelvetia canaliculata* | 21·64 | 0·72 | 3·7 | 0·35 | 565 | 5 | 1·3 | 47 | 2·6 | 38 | 1·2 | 0·2 | >700 | 20 | 22 | 5 |
| *Fucus spiralis* | 24·34 | 1·39 | 6·0 | 0·29 | 638 | 5 | 1·8 | 62 | 1·9 | 27 | 0·9 | 0·2 | >700 | 19 | 104 | 6 |
| *Ascophyllum nodosum* | 19·49 | 0·73 | 4·4 | 0·29 | 283 | 4 | 0·7 | 60 | 1·5 | 26 | 1·0 | 0·2 | >700 | 13 | 27 | 4 |
| *F. serratus* | 21·77 | 0·84 | 3·2 | 0·65 | 375 | 10 | 1·3 | 70 | 2·0 | 20 | 0·7 | 0·3 | >700 | 22 | 155 | 5 |
| *F. vesiculosus* | 23·97 | 0·65 | 3·8 | 0·34 | 221 | 2 | 0·5 | 60 | 1·9 | 28 | 1·8 | 0·2 | >700 | 44 | 116 | 7 |
| *Laminaria digitata* frond | 31·84 | 0·29 | 2·4 | 0·19 | 138 | 2 | 1·0 | 64 | 0·6 | 5 | 0·4 | 0·3 | >700 | 13 | 9 | <3 |
| *L. digitata* stipe | — | 0·92 | 3·9 | 0·10 | 293 | 6 | 1·7 | 62 | 0·3 | 2 | 0·4 | 0·4 | >700 | 15 | 10 | 5 |
| *L. cloustoni* frond | 32·16 | 0·25 | 1·6 | 0·14 | 159 | 12 | 1·4 | 76 | 0·9 | 10 | 1·5 | 0·3 | >700 | 31 | 10 | 14 |

### Table IV. Trace-element Contents of Oven-dried Seaweeds (Collected 27 June 1950) in mg./kg.

| Sample | Total ash (% of dry matter) | Co | Ni | Mo | Fe | Pb | Sn | Zn | V | Ti | Cr | Ag | Sr | Ba | Mn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pelvetia canaliculata* | 23·3 | 1·30 | 4·8 | 0·55 | 2040 | 13 | 2·2 | 90 | 3·2 | 60 | 1·2 | 0·3 | 720 | 34 | 51 | 16 |
| *Fucus spiralis* | 22·8 | 2·00 | 9·3 | 1·32 | 3380 | 5 | N.d. | N.d. | 11·9 | 308 | 3·7 | 0·4 | 420 | 64 | 121 | 31 |
| *Ascophyllum nodosum* | 20·4 | 0·73 | 3·7 | 0·89 | 1150 | 4 | 1·1 | 116 | 2·8 | 28 | 1·9 | 0·1 | 570 | 18 | 36 | 12 |
| *F. vesiculosus* | 19·5 | 0·91 | 5·9 | 0·34 | 730 | 7 | 1·1 | 105 | 1·7 | 27 | 1·5 | 0·2 | 730 | 22 | 102 | 10 |
| *F. serratus* | 18·0 | 0·63 | 4·5 | 0·21 | 320 | 4 | 0·5 | 63 | 0·6 | 7 | 0·7 | 0·2 | 520 | 16 | 120 | 6 |
| *Laminaria digitata* frond | 26·2 | 0·31 | 1·8 | 0·16 | 400 | 7 | 0·6 | 59 | 0·5 | 4 | 1·1 | 0·1 | 690 | 17 | < 30 | 5 |
| *L. digitata* stipe | 38·9 | 0·46 | 3·7 | 0·28 | 1260 | 16 | 2·8 | 92 | 0·7 | 8 | 1·8 | 0·4 | 1150 | 28 | < 30 | 11 |
| *L. digitata* frond, Ardencaple Bay | 29·7 | 0·22 | 2·1 | 0·17 | 410 | 4 | 0·2 | 71 | 0·7 | 4 | 1·8 | 0·0 | 950 | 18 | < 30 | 6 |
| *L. digitata* stipe, Ardencaple Bay | 37·8 | 0·62 | 5·7 | 0·34 | 1570 | 7 | 0·2 | 85 | 1·2 | 5 | 2·9 | 0·0 | 1120 | 20 | < 30 | 21 |

### Table V. Trace-element Contents of Wet Seaweeds (Collected 27 June 1950) in mg./kg.

| Sample | Co | Ni | Mo | Fe | Pb | Sn | Zn | V | Ti | Cr | Ag | Sr | Ba | Mn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pelvetia canaliculata* |  | 1·1 | 0·14 | 473 | 3·0 | 0·51 | 21 | 0·74 | 14 | 0·28 | 0·07 | 167 | 7·9 | 12 | 3·7 |
| *Fucus spiralis* | 0·37 | 1·7 | 0·24 | 622 | 0·92 | N.d. | N.d. | 2·2 | 57 | 0·68 | 0·07 | 77 | 12 | 22 | 5·7 |
| *Ascophyllum nodosum* | 0·17 | 0·92 | 0·22 | 285 | 1·00 | 0·27 | 29 | 0·69 | 6·9 | 0·47 | 0·03 | 141 | 4·5 | 8·9 | 2·9 |
| *F. vesiculosus* | 0·21 | 1·36 | 0·07 | 169 | 1·6 | 0·25 | 24 | 0·39 | 9·2 | 0·35 | 0·05 | 169 | 5·1 | 24 | 2·3 |
| *F. serratus* | 0·12 | 0·87 | 0·04 | 62 | 0·78 | 0·10 | 12 | 0·12 | 1·4 | 0·14 | 0·04 | 101 | 3·1 | 23 | 1·2 |
| *Laminaria digitata* frond, Atlantic Bridge | 0·04 | 0·25 | 0·03 | 56 | 0·97 | 0·08 | 8·2 | 0·07 | 0·56 | 0·15 | 0·01 | 96 | 2·4 | < 4 | 0·7 |
| *L. digitata* stipe, Atlantic Bridge | 0·06 | 0·47 | 0·04 | 160 | 2·0 | 0·36 | 11·7 | 0·09 | 1·0 | 0·23 | 0·05 | 146 | 3·6 | < 3·8 | 1·4 |
| *L. digitata* frond, Ardencaple Bay | 0·03 | 0·36 | 0·03 | 71 | 0·69 | 0·03 | 12·2 | 0·12 | 0·69 | 0·31 | 0·0 | 163 | 3·1 | < 5·2 | 0·9 |
| *L. digitata* stipe, Ardencaple Bay | 0·07 | 0·64 | 0·03 | 176 | 0·78 | 0·24 | 9·5 | 0·13 | 0·56 | 0·32 | 0·0 | 125 | 2·2 | < 3·3 | 2·4 |

## TABLE VI. TRACE-ELEMENT CONTENTS OF SEA WATER IN $\mu$G. PER LITRE

| Sample | Co | Ni | Mo | Pb | Sn | Zn | V | Ti | Cr | Ag | Sr | Ba | Mn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taken 20 miles off Plymouth at 20m. on 22. ii. 50. Stored in Pyrex bottle | < 0·3 | 6 | 12 | < 8 | < 5 | 9 | 2·4 | 8 | 1·2 | 2·9 | N.d. | N.d. | N.d. | N.d. |
| As in (1), but stored in Polythene bottle | < 0·3 | 5 | 12 | < 8 | < 5 | 13 | 2·7 | 9 | 2·5 | 2·1 | N.d. | N.d. | N.d. | N.d. |
| Taken at Ardencaple Bay at ½ m. on 27. vi. 50. Stored in Pyrex bottle | < 0·3 | 1·5 | 12 | < 5 | < 5 | 11 | 5 | 6 | 1·6 | < 0·4 | 10,000 | < 1,000 | < 3,000 | < 3,000 |
| Taken at Atlantic Bridge at ½ m. on 27. vi. 50. Stored in Pyrex bottle | < 0·3 | 1·5 | 16 | < 5 | < 5 | 21 | 7 | 6 | 1 | < 0·4 | 9,000 | < 1,000 | < 3,000 | < 3,000 |
| Noddack (1940)* | 0·1 | 0·5 | 0·5 | 5 | 3 | 14 | — | — | — | 0·15 | — | — | 3 | 4 |
| Ernst & Hoermann (1936)* | | 0·1 | 0·3–0·7 | — | | — | 0·2–0·3 | — | — | — | — | | | |
| Atkins (1936)* | | — | — | — | — | < 8 | — | — | | — | | — | | 10 |
| Haber (1928)* | — | — | — | — | — | | — | — | — | 0·3 | — | — | — | — |
| Goldschmidt (1937)* | — | | — | | — | — | — | — | — | — | — | 50 | | — |

* Quoted from Harvey (1945).

## TABLE VII. 'CONCENTRATION FACTOR', OR RATIO OF TRACE-ELEMENT CONTENT IN ALGAE (FRESH WEIGHT) TO TRACE-ELEMENT CONTENT IN SEA WATER

| Sample | Ni | Mo | Zn | V | Ti | Cr | Sr |
|---|---|---|---|---|---|---|---|
| *Pelvetia canaliculata* | 700 | 8 | 1,000 | 100 | 2,000 | 300 | 20 |
| *Fucus spiralis* | 1,000 | 15 | — | 300 | 10,000 | 300 | 8 |
| *Ascophyllum nodosum* | 600 | 14 | 1,400 | 100 | 1,000 | 500 | 16 |
| *F. vesiculosus* | 900 | 4 | 1,100 | 60 | 2,000 | 400 | 18 |
| *F. serratus* | 600 | 3 | 600 | 20 | 200 | 100 | 11 |
| *Laminaria digitata* frond, Atlantic Bridge | 200 | 2 | 400 | 10 | 90 | 200 | 90 |
| *L. digitata* stipe, Atlantic Bridge | 300 | 3 | 600 | 10 | 200 | 230 | 16 |
| *L. digitata* frond, Ardencaple Bay | 200 | 2 | 1,000 | 20 | 100 | 200 | 18 |
| *L. digitata* stipe, Ardencaple Bay | 400 | 2 | 900 | 30 | 90 | 200 | 14 |

## Acknowledgements

This work forms part of a programme of research and development of the Scottish Seaweed Research Association, and the writers are indebted to the Director for permission to publish. The writers also wish to thank the staff of the Plymouth Marine Biological Laboratory, who collected the water samples off Plymouth, and the staff of the Macaulay Institute for Soil Research, Aberdeen, for the very valuable assistance in carrying out the spectrographic analyses.

## Summary

Some common Scottish Laminariaceae and Fucaceae have been analysed spectrographically, and seventeen of the minor elements determined.

The results show that there is a seasonal variation and considerable variation in the content of these elements in different species taken from the same habitat.

With the Laminariaceae the trace elements are more concentrated in the perennial stipe than in the attached frond, and are generally less than in the Fucaceae.

Samples of sea water taken off Plymouth and the West Coast of Scotland have also been analysed spectrographically and fourteen of the minor elements determined.

Concentration factors are given showing the extent to which marine algae can accumulate the trace elements. Values of over 1000-fold concentration are reported. *Fucus spiralis*, for example, contains 10,000 times more titanium than the surrounding sea water.

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# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### Blood Cell Formation in Certain Teleost Fishes

By **W. T. Catton**

*Journ. Hematology*, Vol. 6, 1951, pp. 39–60

The blood cells of brown trout (*Salmo trutta*) and common roach (*Rutilus rutilus*) are described, and some comparisons are made with the blood cells of the marine teleosts, *Ctenolabrus rupestris* and *Trigla cuculus*. Confirming previous authors, the sites of blood-cell formation in these teleost fishes are chiefly in the intertubular tissue of the kidneys. The structure of the intertubular tissue is described as that of a 'spongework' of reticular cells, with scattered endothelial elements, and enclosing in the meshes large numbers of blood-cell precursor elements in various stages of development. Vascular connexion with the peritubular capillaries is described. On the basis of histological study of the primitive blood-forming cells, a monophyletic scheme of development is proposed, in which the stem cell, derived from a reticular cell, is regarded as a large cell of lymphoid character ('large lymphoid haemoblast'). From cells of this type, the blood granulocytes develop by a process of differentiation. Blood erythrocytes and thrombocytes develop from small lymphoid cells of the same general character ('small lymphoid haemoblasts'). These small lymphoid cells may be derived from the larger cells by mitotic divisions, which are frequently seen. Alternatively, the small lymphoid cells may be derived from endothelial elements of the haematopoietic tissues. On this latter supposition, a close analogy may be drawn with the scheme of blood-cell formation in mammals, according to the work of Doan, Cunningham and Sabin. No evidence of such derivation of the small lymphoid cells could be observed. W.T.C.

### Notes on some Larval Decapods (Crustacea) from Bermuda. II

By **Marie V. Lebour**

*Proc. Zool. Soc. Lond.*, Vol. 120, 1951, pp. 743–7

These notes add to our knowledge of the larval decapods of Bermuda. New facts are given as regards *Amphion* and it is shown that a very late stage brings it nearer to the adult form, which is probably *Amphionides* as Gurney has suggested. A late larva of *Anchistioides antiguensis* (Schmitt) was found in deep-water plankton, and is of great interest as only the first and second larvae are so far known. It is here shown that there is a first larval stage in the hippolytid *Trachycaris*, which corresponds exactly with a similar stage in most other carids, having the eyes covered and the supra-orbital spines still under the skin. M.V.L.

## GIANT AXONS AND SYNERGIC CONTRACTIONS IN *BRANCHIOMMA VESICULOSUM*

By **J. A. Colin Nicol**

*Journ. Exp. Biol.*, Vol. 28, 1951, pp. 22–31

The giant axons of the sabellid worm *Branchiomma vesiculosum* mediate quick synergic contractions of the longitudinal musculature. The neuromuscular functioning of this system was investigated by means of electrical stimulation (condenser discharges) and graphical recording. Single muscle-twitches occur at stimulation frequencies up to 2 per second, above which clonus, and finally tetanus result. At high rates of stimulation fatigue rapidly sets in; this fatigue is reversible. Maximal tension is developed about 255 msec. after the beginning of contraction, and relaxation occupies about 1·8 sec. With an isometric lever it has been shown that under repetitive stimulation maximal tension is developed initially, and there is no evidence for the existence of peripheral facilitation. The paper concludes with a discussion of the results in terms of the natural habits of the animal. J.A.C.N.

## ON A GIANT SQUID, *OMMASTREPHES CAROLI* FURTADO, STRANDED AT LOOE, CORNWALL

By **W. J. Rees**

*Bull. Brit. Mus. (Nat. Hist.), Zool.*, Vol. 1, 1950, pp. 31–41

A large specimen of the giant squid, *Ommastrephes caroli* Furtado, was stranded in live condition in November 1940. Standard measurements are given, together with a detailed account of the dentition of the sucker rings. Female specimens only are known. Most strandings occur along the east coast of Britain, with main strandings at Scarborough, the Dunbar-North Berwick area and at Buckie.

All authenticated records of this and other giant squids (*O. pteropus* and *Architeuthis* spp.) have been collected and plotted on maps. It appears that these species are oceanic forms which occasionally migrate into the North Sea and become enfeebled by unfavourable conditions during the winter months. The scanty evidence we now possess suggests that the adult squids inhabit the continental slope beyond the 100-fathom line. Two excellent photographs by Dr D. P. Wilson are included in the report. W.J.R.

## ON THE BEHAVIOUR OF *SABELLA*

By **G. P. Wells**
Department of Zoology, University College, London

*Proc. Roy. Soc.*, B, Vol. 138, 1951, pp. 278–99

The water currents which *Sabella spallanzanii* and *S. pavonina* drive through their tubes vary with time according to definite and characteristic patterns. These are described in detail, and the bearing of the results on the general physiology of the worms is considered.

In either species, the tube consists of a stiff stem and a more flexible root, and is open at both ends. The opening of the stem (anterior opening) is always well above the substratum. That of the root (posterior opening) was found to be above the surface of the substratum in *S. spallanzanii* but embedded in the mud in *S. pavonina*. This means that the tube can easily be irrigated in either direction in *S. spallanzanii* but tailwards only in *S. pavonina*.

Both species irrigate their tubes vigorously, whether the crown is expanded or withdrawn. In *S. spallanzanii*, pauses are brief and rare; the direction and velocity of irrigation often change and certain characteristic patterns are constantly reproduced. In *S. pavonina* there may be pauses of over an hour's duration and irrigation is tailwards only. The fact that the former species irrigates in either direction and the latter in one direction only is clearly correlated with the difference in form of their tubes. As the worms were studied under identical mechanical conditions, the behaviour difference is inherent.

Decapitation (removal of crown, collar and part or all of the thorax) has very little effect on the irrigation behaviour of either species. This suggests that the crown is unimportant as a respiratory organ.

A worm may still be very active, even though its crown is withdrawn into its tube. The suggestion is made that feeding may occur from the irrigation current when the crown is withdrawn. G.P.W.

## THE INTEGRATION OF ACTIVITY CYCLES IN THE BEHAVIOUR OF *ARENICOLA MARINA* L.

By **G. P. Wells** and **Elinor B. Albrecht**

*Journ. Exp. Biol.*, Vol. 28, 1951, pp. 41–50

Two distinct cyclic behaviour patterns are known to be important in the normal life of the lugworm: the feeding cycle of period about 6–7 min., originating in the oesophageal wall (*f* cycle), and the irrigation-defaecation cycle of period usually about 40 min., and probably originating in the nerve cord (*i-d* cycle). The integration of these two patterns was studied in a series

of dissected preparations. Neither pacemaker directly affects the rhythm of the other. The integration of the activities which they determine depends on variation in the extent to which their influences spread through the neuromuscular system. They appear to compete for territory. If they happen to discharge outbursts simultaneously, the *i-d* pacemaker dominates over most of the body wall, and the *f* pacemaker over the proboscis and mouth region.
G.P.W.

## The Role of Oesophageal Rhythms in the Behaviour of *Arenicola ecaudata* Johnston

By **G. P. Wells** and **Elinor B. Albrecht**

*Journ. Exp. Biol.*, Vol. 28, 1951, pp. 51–6

The brainless isolated extrovert of *A. ecaudata* traces a continuous, or nearly continuous, background of activity, upon which prominent spells of vigorous rhythmic contraction appear at intervals of the order of 30–40 min. Similar spells are sometimes shown by the corresponding preparation from *A. marina*, whose characteristic *f* cycle can be regarded as produced by the organization of the background activity of *ecaudata* into vigorous and regularly spaced outbursts. There is little evidence of a pacemaker role of the oesophagus in *ecaudata*. G.P.W.

# CLASSIFIED LIST OF PUBLICATIONS

## VOLUMES XVI TO XXIX OF *THE JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION* AND OTHER PUBLICATIONS RECORDING THE RESULTS OF RESEARCHES CARRIED OUT AT THE PLYMOUTH LABORATORY FROM 1928 TO 1950

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# PREFACE

It is now 25 years since I produced the 'List of Publications' in Volume XV of this Journal,[1] which brought the earlier 1913 list up to date.

Much has been published since then and there is an evident need for a supplementary list. Accordingly, Mr N. A. Holme has prepared the following classified list of the contents of Volumes XVI to XXIX of the *Journal of the Marine Biological Association* and of other publications recording the results of researches carried out at the Plymouth laboratory from 1928–1950.

The last list only recorded those publications containing research carried out under the auspices of the Marine Biological Association. Since 1927, however, an increasing number of papers have been published in the Journal dealing with research at other marine biological laboratories in the British Isles. It is felt that the inclusion of such papers is valuable, not only in supplying a complete index of contents to the Journal volumes concerned, but as a useful bibliography to much marine biological literature.

There has been some rearrangement in this new list. Papers dealing with general biological problems have been placed first, followed by papers on the biology of different groups. As previously an authors' index has been provided, from which can be obtained the section and reference number of any paper.

Within each section or subsection the papers have been arranged in date order. Cross-references between sections are given, but, in Sections XII to XXX, there are none between the various subsections of each main section.

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[1] List of Publications recording the results of researches carried out under the auspices of the Marine Biological Association of the United Kingdom in their laboratory at Plymouth or on the North Sea Coast from 1886–1927. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 753–828, 1928.

F. S. R.

*March* 1951

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*See also:* Symbiotic algae of corals, XIII, 6.

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*See also:* Parasites of Mollusca, XXV A, 22–4, B, 37, 39; Parasitic worms from fish, XXIX D, 7.

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## XXX. REPTILIA, AVES, MAMMALIA

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